Information use during foraging by New Zealand bellbirds (*Anthornis melanura*)

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Jennifer May Dent

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Nectivorous foragers rely on patchily distributed, static resources of highly variable quality. The ability to learn and remember information concerning the spatial distribution of available resources, and to associate this with variation in resource quality, is an adaptive trait for many nectivorous species. I examine informed foraging in regard to the New Zealand bellbird (*Anthornis melanura*). Bellbirds are facultative nectarivores; although they demonstrate an affinity for nectar, they readily switch to alternate food sources when it is unavailable. Informed foraging by nectarivores has largely been examined with respect to more highly specialised species (e.g. Trochilidae). Focus on a facultative nectarivore allows for examination of cognitive constraints in a less specialised system, where the availability of nectar poses fewer restrictions on forager behaviour.

The first part of this thesis explored information use in natural environments by assessing engagement in resource tracking by bellbird populations at two spatial scales (Chapter 2-3). At a local scale, the nectivorous activity of resident bellbirds within 1 ha plots of native bush was correlated with spatial patterns of flowering for four key nectar species. The strength of the tracking response observed was linked to the pollination syndrome of the focal plants. Availability of ornithophilous plant species elicited stronger and more consistent tracking responses than the availability of entomophilous species. At a larger, landscape scale the movements of seasonally transient birds

were quantified using a dialectal song type matching technique. Dispersal was found to be more distance limited than previously assumed. This suggests that large scale resource tracking may operate at an intermediary patch scale, rather than at a landscape scale.

The second part of this thesis examined the cognitive mechanisms that may underlie informed foraging behaviours. I performed a series of experimental feeder trials on free-living male bellbirds (Chapter 4-6). Trials examined the ability of individuals to return to the location of a highly rewarding feeder within an array of less rewarding feeders. Treatments varied with respect to the reward concentration, the duration of the withholding period, the presence of visual cues, and the size of the experimental array. Bellbirds were found to have accurate spatial memory. Individuals were able to relocate rewards across a range of concentration treatments, retain spatial information for periods of up to 20 days, learn to associate visual cues with reward characteristics, and use spatial cues in a scale dependent manner.

Overall, my research indicates that bellbirds were capable of engaging in memory informed foraging on nectar resources. Targeted exploitation of resources across multiple spatial scales likely translates to increased foraging efficiency. Low dietary dependence on nectar is associated with flexible usage of informed foraging, rather than a lack of cognitive ability in this species.

Keywords: facultative nectarivores, memory informed foraging, resource tracking, resource value, spatial memory, visual cues

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George Weasley, the bellbird

Photo: Jennifer Dent

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Chapter 1

Introduction

1.1 Information use in foraging

Animals will always be faced with some degree of uncertainty when foraging in a natural environment (Stephens 2007). Resource quality and availability vary according to multiple different spatiotemporal scales, and this variability can be further exacerbated by stochastic events, such as unusual weather. Early foraging models, including the classic "diet" and "patch" models, assumed that foragers had complete knowledge of their foraging environment and were able to exploit the environment in an optimal fashion (Stephens & Krebs 1986; Scheiner & Willig 2011). The diet model, which analysed the decision of predators to attack a prey item or to continue searching, was reliant on the assumption that foragers understood the abundance and ease of locating various prey types, as well as the associated handling time and value of each type (Stephens & Krebs 1986). The patch model explored how long a forager should invest in exploiting a resource with diminishing returns before moving on to the next resource. This model also relied on the assumption that a forager understands the distribution and relative quality of other resources in the environment (Stephens & Krebs 1986).

In reality, it is impossible to have complete knowledge of every relevant environmental feature in a natural foraging situation (Stephens 2007). This is known as the 'problem of incomplete information' (Stephens 2007). When foraging, animals in a state of 'incomplete information' are reliant on estimations of the key environmental parameters to guide foraging decisions (Dall et al. 2005; Scheiner & Willig 2011; Dunlap & Stephens 2012). The estimation process is usually guided by an individual's prior experience: the more knowledgeable or informed an individual is about the current

state of the environment, the more accurate the estimation process tends to be (Dall & Johnstone 2002).

Successful integration of environmental information into behavioural decision making is a two part process. Initially an individual must use experience to acquire information about the current state of the environment (Dunlap & Stephen 2012). In the context of foraging, information refers to any acquired knowledge of resource characteristics, e.g. location, quality, current availability (Stephens 2007; Dunlap & Stephens 2012). There are a range of information sources available to foraging animals. Information that is generated via direct interaction with the environment is known as "personal information", e.g. quality of a resource at the time of the last visit (Dall et al. 2005). Information may also be obtained indirectly by monitoring behaviour of conspecifics, "socially acquired information", e.g. duration of a conspecific's foraging bout as an indicator of quality (Dall et al. 2005). Once information has been acquired, some of it is encoded and stored as a memory (Dunlap & Stephen 2012). Memorised information can then be retrieved in a relevant context in order to inform decision making and subsequent behaviour (Fagan et al. 2013). The collection and use of information by animals is highly dependent on the associated costs and benefits.

1.2 Value of information

Informed foragers are able to exploit the environment in an optimised fashion, which can increase foraging efficiency and individual fitness. The benefit of information is exemplified in cases of juvenile and non-local individuals. Juvenile individuals often lack experience of the environment and must invest time and energy into information acquisition. Haug et al. (2015) demonstrated that young Corys Shearwaters (*Calonectris borealis*) were more exploratory in their foraging behaviour, and visited less productive areas, than older, more experienced foragers. These findings indicated that as birds aged, and gained experience in the local environment, they adopted more efficient foraging movements (Haug et al. 2015). Non-local individuals face a similar lack of information that

limits resource exploitation of novel environments. Pinter-Wollman et al. (2009) studied behaviour of resident and translocated African elephants (*Loxodonta africana*). Translocated elephants spent less time foraging, and more time searching, than resident individuals, which translated to higher mortality and poorer body condition (Pinter-Wollman et al. 2009).

Juveniles and non-local individuals represent extreme cases of uniformed foraging. In most cases information use is a matter of expanding upon, or updating, the current information state and in these situations the value of information is more likely to be mitigated by associated costs. Information use can be costly because animals must divert resources, including time, energy, and attentional capacity towards gathering, storing and updating information (Clark & Dukas 2003; Stephens 2007). These processes can also increase individual exposure to adverse environmental conditions or negative interference, e.g. predation (Dall et al. 2005; Hall et al. 2007; Webster & Laland 2008). Acquisition or retention of inaccurate information can also translate into maladaptive foraging decisions (Cronin 2013). Information use is valuable only when knowledge leads to a change in behaviour that has a net positive consequence for individual fitness (Dall et al. 2005). The potential value of information can be affected by many factors, including resource distribution and characteristics (Stephens 2007; Webster & Laland 2008, Bracis et al. 2015), and individual traits (Webster & Laland 2011; Araya-Salas et al. 2018).

Variation in information value is difficult to study directly as it can be difficult to distinguish between an uninformed state, in which an individual is ignorant of resource states, and an unmotivated state, in which an individual knows the state of resources but chooses not to alter their behaviour in response (Wilkie et al. 1999). The trade-off between personal information and social information is a good model for examining variable information value. Reliance on personal information versus social information often represents a trade-off between accuracy and cost as personal information is generally more accurate but also more costly to acquire (Webster & Laland 2008; Dall et al. 2005). Increased reliance on social information has been demonstrated in empirical studies where

information acquisition costs are high, for example due to high predation risk (Webster & Laland 2008), or in cases where personal information is of low value, such as in cases where resources are highly variable and personal information may quickly become unstable and unreliable (Coolen et al. 2005; Smolla et al. 2016).

1.3 Adaptive specialisation

In situations where information is valuable, foraging efficiency may be constrained by limitations on an individual's ability to acquire and retrieve this information. Information acquisition is constrained by an individual's ability to perceive and experience the foraging environment. Perceptual limitations arise directly when valuable information cannot be accurately registered by a forager's sensory system, e.g. inability to respond to specific odours due to limitations with olfactory acuity (Cunningham et al. 2003). Goulson et al. (2007) studied flower choice by foraging honeybees (*Apis mellifera*) and bumble bees (*Bombus hortorum*) and found that both species used obvious visual cues (colour, petal blemishes) to selectively visit flowers but were only able to respond to subtle cues (robbing holes) at close range. Visual acuity, therefore, limited information use at larger scales (Goulson et al. 2007). Perceptual limitations may also arise indirectly when behavioural constraints limit the experience of an individual. Hall et al. (2007) examined patch sampling behaviour in eastern chipmunks (*Tamias striatu*) and determined that individuals sampled more distant resource patches at a lower frequency. Lower sampling of distant patches was attributed to the higher risk of predation and negative conspecific interactions (Hall et al. 2007).

Even if information is acquired, retention and retrieval of information is limited by the cognitive competency of the forager. The ability of an individual to reliably encode, store, and retain information is constrained by the presence of suitable neural pathways and brain structures (Stephens et al. 2007). The hippocampus, which plays an important role in the storage of spatial information, is a key example of a brain structure that limits information use (Stephens et al. 2007).

Healy & Krebs (1992) demonstrated that variation in the extent of caching behaviour, which requires accurate retrieval of spatial information, correlates with hippocampal volume across seven corvid species. Hippocampal volume has also been linked to variation in spatial memory across populations (Croston et al. 2015), sexes (Clayton & Reboreda 1997) and seasons (Lázaro et al. 2018).

As information acquisition and retrieval can constrain foraging efficiency, the mechanisms that enable these processes are subject to natural selection pressures. Foragers experience unique selection pressures on the basis of their informational requirements that can result in adaptive specialisation. Classes of foragers often evolve similar traits. Hutcheon et al. (2002) studied adaptive specialisation in relation to foraging strategy across 63 bat species. Species were classified as either phytophages (frugivores and nectarivores) or insectivores (Hutcheon et al. 2002). Phytophages rely on olfactory and spatial information to locate resources and, as a result, have enlarged olfactory bulbs and hippocampi (Hutcheon et al. 2002). Insectivores primarily use echolocation to locate prey and have enlarged auditory nuclei (Hutcheon et al. 2002). Specialisation also occurs within foraging classes in response to species specific requirements, e.g. closely related parasitoid wasps species learn olfactory associations at different rates, via different consolidation mechanisms, in response to variation in host plant distributions (Smid et al. 2007). In this thesis specialisation for informed foraging is examined in the context of avian nectarivores.

1.4 Nectivory and information use

Nectar is a sugar-rich aqueous secretion produced in plant glands called nectaries (Pacini & Nepi 2007). Nectar produced in floral nectaries functions as a reward for pollinating animals, whereas nectar produced in extra-floral nectaries functions as a reward for animals that participate in plant defence (Pacini & Nepi 2007). The precise composition of nectar varies, but in all cases comprises simple carbohydrates in the form of sucrose and hexose sugars, and small amounts of amino acids, dissolved in water (Heil 2011). The chemical (e.g. dominant sugar type) and physical (e.g. viscosity,

volume, production rate) properties of nectar are usually determined by consumer identity and consumption characteristics.

Nectar availability has complex spatial and temporal dynamics. At a community level, different plant species adopt different production strategies, giving rise to variation in composition, rate of production, and temporal availability (Rathcke 1992; Fonseca et al. 2015). Within plants of the same species variation in production can arise through genetic variation, environmental conditions or plant characteristics, e.g. dioecy and age (Rathcke 1992; Adgaba et al. 2017). Furthermore, within individual plants, rewards may be inconsistent due to depletion by conspecifics, floral age, stage, or position (Rathcke 1992; Lu et al. 2015). Reliance on a static resource of highly variable quality has selected for efficient use of spatial information in many nectivorous species (Garber; 1988; Cartar 2004; Pérez et al. 2011; Henry & Stoner 2011). Retention of spatial information allows for revisitation of important or high quality feeding sites (Henry & Stoner 2011), and when coupled with information of the state of the resource at the time of the last visit, this can greatly improve foraging efficiency (González-Gómez et al. 2011; Fagan et al. 2013).

Empirical studies have demonstrated that reliance on spatial memory abilities is widespread throughout the nectarivore guild, including cases from insects (Menzel et al. 2005), bats (Henry & Stoner 2011), and birds (González-Gómez et al. 2011). Due to the difficulty of manipulating nectar resources in the field, most studies of memory-informed nectar foraging have been conducted under laboratory conditions, or in fine scale field experiments (Hurly & Healy 1996; Burke & Fulham 2003; Henderson et al. 2001; Sulikowski & Burke 2011; Marshall et al. 2012; Whitfield et al. 2014; Samuels et al. 2014). Though these studies provide insight into the cognitive mechanisms that underpin foraging behaviour, their applicability to natural foraging has limits. A natural foraging environment is usually much more complex than any laboratory set up. Not only is the resource diversity higher (in terms of quality, availability and type) but the resources are dispersed over a much larger area.

The application of spatial information in natural environments is less well understood for foraging nectarivores. In natural conditions, spatial patchiness of nectar is hierarchical as flowers are clumped within individual plants (individual), plants are nested within sites (local), sites are grouped within regions (landscape), and regions form parts of wider geographical areas (geographical) (García & Ortiz-Pulido 2004). Nectar production for a species may vary at all of these levels. One of the most effective tools for studying information use across each spatial scale is the examination of forager movements in relation to the distribution of nectar resources. In cases where search behaviour is driven by memory informed foraging, directed, non-random foraging movements are expected (Fagan et al. 2013; Bracis et al. 2015). At a local scale, individuals have been observed to engage in trapline foraging which involves making repeated sequential visits to a series of feeding locations (Garrison & Gass 1999; Thomson et al. 1997), or form map-like representations which allow flexible pathfinding within their foraging environment (Menzel et al. 2005). Local populations also exploit nectar resources in a non-random manner via resource tracking (Cotton 2007; Guitián & Munilla 2008). At larger spatial scales, the dispersal behaviours of species have been linked to temporal changes in the landscape distribution of nectar (Kuiper et al. 2015). The expression of information as targeted movements at each spatial scale is constrained by both the perceptual and mobility limitations of foragers.

1.5 Avian nectarivores

There are three main lineages of nectar feeding birds worldwide; the hummingbirds (Trochilidae) of North and South America, the sunbirds (Nectariniidae) of Africa and Asia, and the honeyeaters (Meliphagidae) of Australasia (Nicholson & Fleming 2003). Adaptation for nectar feeding evolved independently in each of these groups and has resulted in differing levels of specialisation (Nicholson and Fleming 2003; Fleming and Muchhala 2007). Hummingbirds are the most phenotypically specialised taxa, followed by sunbirds and then honeyeaters (Pyke 1980, Fleming and Muchhala 2007; Nicholson and Fleming 2014). Hummingbirds have been extensively studied in regards to

informed foraging. Individuals have been shown to remember information concerning the content and schedule of nectar production for individual flowers, and use this information to avoid unrewarding sites and return to profitable ones (Henderson et al. 2001; González-Gómez & Vásquez 2006; González-Gómez et al. 2011; Pérez et al. 2011; Jelbert et al. 2014). The advanced cognitive ability of hummingbird species is generally attributed to their specialisation for nectivory (Healy & Hurly 2003; Araya-Salas et al. 2018). Hummingbirds have high mass-specific metabolic demands so visiting a low value or depleted resource has large metabolic consequences (Beuchat et al. 1990). The high cost associated with visiting a low value resource has likely selected for extensive and accurate spatial memories (Healy & Hurly 2003; Araya-Salas et al. 2018).

Relatively little research has been undertaken examining memory informed foraging in sunbirds and honeyeaters. Two Australian honeyeater species, the regent honeyeater (*Anthochaera phrygia*) and noisy miner (*Manorina melanocephala*) have been shown capable of remembering fine scale spatial information about nectar rewards (Burke & Fulham 2003; Sulikowski & Burke 2007). Captive studies demonstrated that individuals from both species were able to avoid recently depleted experimental flowers (Burke & Fulham 2003; Sulikowski & Burke 2007) and, in the case of regent honeyeaters, return to them after longer intervals (Burke & Fulham 2003). Noisy miners were also able to remember and avoid specific sites within arrays that were unprofitable (Sulikowski & Burke 2010), and associate colour cues with a reward (Sulikowski & Burke 2015). Amethyst sunbirds (Chalcomitra amethystina) have also been shown to associate colour cues with a reward (Whitfield et al. 2014).

Relatively low representation of sunbirds and honeyeaters in cognitive studies is in part because their behaviour has been viewed as less easily applicable to fine scale mechanistic studies, and because of their lower levels of specialisation which would suggest lower levels of adaptive specialisation (Henry & Stoner 2011; Whitfield et al. 2014). As most nectarivores exploit nectar on a facultative rather than an obligate basis (Zanata et al. 2017), it is important to examine information

use in nectar foraging in less specialised systems. In this thesis, I shall examine information use in reference to a honeyeater, the New Zealand bellbird (*Anthornis melanura*).

1.6 Avian nectivory in New Zealand

Ornithophily is rare in New Zealand and less than 1% of the indigenous New Zealand flora produce flowers that are typical of the ornithophilous syndrome, e.g. large nectar volume, vivid floral display, and tubular shape (Lloyd 1985; Cronk & Ojeda 2008). Prior to the arrival of humans in New Zealand, five endemic bird species carried out the majority of avian pollination; two honeyeater species, the tūī (*Prosthemadera novaeseelandiae*) and the bellbird, as well as hihi (*Notiomystis cincta*), kaka (*Nestor meridionalis*) and saddleback (*Philesturnus carunculatus*) (Anderson et al. 2006). Due to human impacts, including habitat reduction and the introduction of mammalian predators and herbivores, these species are largely absent from the New Zealand mainland (hihi, saddleback) or exist within a smaller range at lower densities (kaka, tūī, bellbird) (Anderson et al. 2006). The vast majority of floral visitation events are now performed by the two honeyeater species, and the recently self-introduced opportunistic nectarivore, the silvereye (*Zosterops lateralis*) (Kelly et al. 2006). This study will focus on bellbirds, the most widespread honeyeater in New Zealand's South Island (Heather & Robertson 2015). Bellbirds are smaller and less dominant than their tūī counterparts and consume a more highly varied diet (Gravatt 1971; Craig 1985; Rasch & Craig 1988). Neither species has been the focus of any prior foraging cognition research.

1.7 Bellbirds

Bellbirds (or korimako) are medium sized (males 34 g, females 25 g) endemic New Zealand honeyeaters (Heather & Robertson 2015). They are common in many parts of New Zealand's South Island, and in some forests and offshore islands on the North Island (Heather & Robertson 2015). Sexes can be determined by plumage. Adult males are olive green in colour with sheen of iridescent purple around their heads and bluish black around their wings and tails. Female birds are olive-

brown in colour with little differentiation between body, wings or head. Females have a distinctive pale yellow stripe which runs from the base of the bill to below the eye. Both males and females are active singers, although males have a wider repertoire of songs and are more vocally active outside of the breeding season (Brunton & Li 2006). Bellbird song is known to play an important role in competitive interactions and resource defence in both sexes (Brunton & Li 2006; Brunton et al 2008b), and further, as a means of mate acquisition in males (Brunton & Li 2006). Geographical variation in song type has been reported and provides a means to examine dispersal behaviour (Brunton et al. 2008a).

Like other honeyeater species, bellbirds have morphological adaptations to nectar feeding, including a slightly decurved bill and a protrusile brush tipped tongue (Heather & Robertson 2015). Bellbirds are versatile in their feeding habits, but preferentially consume nectar when available (Spurr et al. 2011; Gravatt 1971). Preferred native nectar sources of New Zealand bellbirds include kohekohe (*Dysoxylum spectabile*), fuchsia (*Fuchsia excorticata*), rewarewa (*Knightia excelsa*), lowland flax (*Phormium tenax*), small-leaved kowhai (*Sophora microphylla*), and puriri (*Vitex lucens*) (Spurr et al. 2011; Gravatt 1971). Foraging bellbirds have been observed to utilise plant species independently of their availability, especially with regard to nectar producing species (Spurr et al. 2011).This may indicate engagement in informed foraging movements. When nectar is scarce, especially in late summer through to early winter, bellbirds will adopt a largely frugivorous or insectivorous diet depending on local availability (Gravatt 1971; O'Donnell & Dilks 1994; Spurr et al. 2011). Females in particular, are known to be highly insectivorous (Gravatt 1971), especially during the breeding season which extends from late spring to mid-summer (October – January) (Craig et al. 1981; Anderson & Craig 2003). During the breeding season bellbirds may raise multiple clutches of up to four eggs (Anderson and Craig 2003). Nest building and incubation is performed by the female only, but both parents participate in chick provisioning (Anderson and Craig 2003).

Bellbirds may attempt to defend key nectar resources year-round (Craig & Douglas 1986). In cases where exclusive resource defence is not viable, e.g. due to high competition for resources, individuals may defend part of a tree from other competitors (Craig & Douglas 1986) or engage in temporal partitioning (Craig & Douglas 1984). Aggressive interactions between individuals are mediated by an intra-species dominance hierarchy (Craig 1984; Craig 1985). Male birds are typically dominant over female birds, which are in turn dominant over juvenile birds (Craig & Douglas 1986).

Bellbirds are highly mobile and capable of dispersing over large distances (Brunton et al. 2008a). This mobility varies seasonally, and can be constrained by social factors. Bellbirds retain territories during their breeding season, sometimes returning to the same breeding grounds between years (Anderson & Craig 2003; Brunton et al. 2008b). Territory sizes have not been quantified for bellbirds but are likely highly dependent on population density and habitat characteristics (Spurr et al. 2010). Home range estimates during the breeding season have been quantified in two studies with contrasting results. Anderson & Craig (2003) showed that the average area over which pairs on Tiritiri Mātangi ranged was only 0.02 ha, whereas Spurr et al. (2010) demonstrated that in a lower density population in Canterbury, home range sizes were much larger, up to 3.7 ha. Despite territorial behaviour during the breeding season, home range overlap was reported in both studies (Anderson & Craig 2003; Spurr et al. 2010). Individuals have also been observed to fly at least 500 m from their core home ranges to exploit nectar resources (Spurr et al. 2010). Outside of the breeding season they are usually solitary and disperse over greater distances (Spurr et al. 2011; Heather & Robertson 2015). Different studies have found disparate results in gender bias of non-breeding season movements. Craig and Douglas (1984b) found that males moved further and more often, whereas Sagar (1985) found females and juveniles to be more mobile.

1.8 Thesis structure

In this thesis I explore information use and cognition in relation to free-living New Zealand bellbirds. Bellbirds, despite bearing some morphological adaptations to nectar feeding, occupy a facultative nectar feeding niche that makes them good candidates for study of cognitive specialisation in a less specialised system. Previous work on honeyeaters has focused at a fine scale, primarily on the win-shift response in which foragers avoid depleted floral resources over short timescales (Burke & Fulham 2003; Sulikowski & Burke 2007; Sulikowski & Burke 2010). Win shift strategies are most beneficial when foraging at small spatial scales, e.g. between profitable and unprofitable flowers.

In this thesis, my focus is on cognitive specialisation of facultative nectarivores when foraging at larger spatial scales, e.g. between plants or resource patches, and over longer timescales, e.g. days, weeks, seasonal. At these larger scales, a win-stay strategy, the ability to return to high value resources, is likely to have a bigger role to play than at lower scales. At a species level, research on how bellbirds interact with their food sources and the cognitive demands of their foraging niche is beneficial as it provides insights into the underlying drivers of individual behaviours and population trends.

My thesis is designed in two parts. In part one I examine bellbird movements at a population level in order to determine whether bellbirds engage in tracking of nectar resources. Bellbirds are a mobile species (Spurr et al. 2010) and forage non-randomly for nectar in their local environments (Spurr et al. 2011), I expected that, provided they were sufficiently motivated, bellbirds would track nectar availability at these larger spatiotemporal scales. In part two, I perform a series of experimental feeder trials on wild birds in order to examine the potential mechanisms that may underlie natural foraging behaviours. Given that many nectivorous species rely heavily on spatial memory, I expected that bellbirds would demonstrate a similar aptitude for use of spatial information. This prediction is

supported by Spurr et al. (2010) who observed individuals making targeted, long distance (> 500 m) flights to out of sight nectar resources.

1.8.1 Part One

Objective: Evaluate movements of bellbirds in relation to spatiotemporal variation in nectar availability [Chapters 2 & 3].

In **Chapter Two**, I examine local spatial and temporal resource tracking within two 100 m x 100 m plots in forested reserves on the Christchurch Port Hills. In the analysis I considered the individual spatial distributions of nectar producing species. This allowed motivational differences to be considered when interpreting observed bellbird distributions.

In **Chapter Three**, I examine resource tracking at a larger scale. Bellbirds move from the Port Hills to Christchurch City on a seasonal basis, which has been hypothesised to relate to the flowering of adventive species within Christchurch City. I used variation in song type to determine the source population of transient, urban birds which allowed for quantification of the dispersal movements.

1.8.2 Part Two

Objective: Assess the ability of bellbirds to retain spatial and visual information about artificial food sources [Chapters 4, 5 & 6].

In **Chapter Four**, I discuss a series of experiments which examined whether bellbirds were able to remember fine scale spatial information when visiting an array of artificial sugar water feeders, and whether the observed cognitive response was dependent on the reward characteristics. This study was the first to examine the role that reward value plays in mediating short term and long term accuracy of spatial memories in nectivorous birds.

In **Chapter Five**, I discuss a second set of experimental trials, which had a similar design to those in Chapter Four, but introduced a visual cue which was a reliable indicator of reward value. In this chapter I examine whether bellbirds were able to learn to use a visual cue, and which form of information, spatial or visual, was given priority.

In **Chapter Six**, I discuss a pilot study which manipulated the size of experimental arrays in order to determine whether cue use was scale dependant. Of particular relevance to this study was the use of relative or absolute spatial information.

This thesis has been written as a series of five stand-alone research items intended for future publication (Chapters 2 – 6). As a result there is some repetition in the introduction and methodology sections of the various chapters. Chapter 7 provides a general discussion of key findings from my research. All references and appendices are provided at the end of the thesis. Research from Chapters 2, 3, 4, and 5 will be submitted for publication as multi-authored papers in collaboration with members of my supervisory committee. Chapter 6 will be submitted as single author short communication. All text was written by me, though I have benefited from edits suggested by members of my supervisory committee. Analysis was also primarily carried out by me, with the exception of the NMDS analysis in Chapter 3 which was carried out by Jon Sullivan.

Chapter 2

Spatiotemporal resource tracking at a local scale by New Zealand bellbirds (*Anthornis melanura*)

2.1 Abstract

Tracking spatiotemporal variation in resource availability allows a forager to more efficiently exploit variable resources, such as nectar. Resource tracking by New Zealand bellbirds (*Anthornis melanura*) was examined at a local, 1 ha scale. Two 100 x 100 m plots located on the Port Hills of Christchurch, New Zealand were monitored monthly between June 2015 and May 2016. Plots were subdivided into 25 grid cells. Each month the availability of floral resources and bellbird activity was assessed with reference to these grid cells. Floral availability was calculated separately for each of the four key native nectar resources in the area; five finger (*Pseudopanax arboreus*), kowhai (*Sophora microphylla*), fuchsia (*Fuchsia excorticata*) and flax (*Phormium* sp.). Floral availability was correlated with activity in many instances, indicating that bellbirds were capable of spatially tracking resources at a local, 1 ha scale. The spatial tracking response was most consistent for resources typical of the bird pollinated syndrome, indicating that resource tracking was flexible, and dependant on resource value. Monthly bellbird abundance was calculated to determine whether bellbirds were tracking the temporal availability of nectar within the study plots. Temporal correlation between bellbird abundance and floral availability was observed at an annual scale but not within the flowering season. This may indicate that bellbirds were tracking the availability of exotic nectar in the nearby urban/suburban areas of Christchurch, but may also be explained by behavioural shifts associated with the end of the breeding season.

2.2 Introduction

Foragers that rely on spatio-temporally variable food resources often engage in resource tracking behaviours in order to improve foraging efficiency. Resource tracking is associated with non-random exploitation of the foraging environment, as foragers concentrate effort in areas with the greatest resource availability across a variety of scales (Franklin & Noske 1999; Cotton 2004; Blendinger et al. 2015). Tracking behaviour is widespread and has been reported in all foraging guilds that experience spatial or temporal shifts in resource availability, notably including nectarivores (Franklin & Noske 1999; Cotton 2004) and frugivores (Garcia & Ortiz-Pulido 2004; Saracco et al. 2004; Guitian & Munilla 2007; Hamilton et al. 2017), and, to a lesser extent, granivores (Renton et al. 2001), insectivores (Johnson & Sherry 2001), and scavengers (Schlacher et al. 2013).

Resource tracking is thought to be adaptive in many contexts because it can increase the efficiency of resource exploitation and allow species to persist in lower quality environments (Blendinger et al. 2015). Investment in tracking behaviour can, however, come at a cost to individual fitness. In addition to the energetic costs of daily or seasonal tracking movements, individuals must invest energy into monitoring the status and distribution of available resources (Stephens 2007). Tracking movements may further be associated with an increased risk of predation or decreased likelihood of mating success (Stephens 2007). Foragers should only track resources if the benefit of doing so outweighs the potential costs. Tracking costs and benefits are often scale dependant and are heavily influenced by species specific factors.

Species vary greatly in their ability to track resources due to the role of behavioural constraints (Franklin & Noske 1999; Saracco et al. 2004; Hart et al. 2011). Two characteristics, mobility and diet specialisation, are known to play a large role in determining whether or not species engage in resource tracking (Gleditsch et al. 2017). The ability to move freely between resources is important, as only highly mobile individuals are able to monitor and adapt to resource variation (Gleditsch et al.

2017). Mobility can be constrained across various spatial scales by physiological or behavioural limitations, e.g. territoriality and competition (Hart et al. 2011; Bennet et al. 2014). While mobility determines the ability of an individual to adapt to variation in resource availability, diet specialisation determines the value of doing so. Species and individuals vary in terms of how reliant they are on a particular resource. Highly specialised or obligate consumers are constrained to track resources as they must invest effort into tracking these resources in order to survive (Wallace 2005; Stewart & Dudash 2017; Hamilton et al. 2017). Generalist or facultative consumers are able to switch to alternative resources during periods of shortage and typically weakens the resource tracking association as it is not necessary for survival (Mourthé 2014, Kuiper et al. 2015; Stewart & Dudash 2017). Several empirical studies have demonstrated the variable extent of resource tracking by specialist and generalist consumers (Franklin & Noske 1999; Blendinger et al. 2012; Kuiper et al. 2015), but few have examined the variable processes which may drive tracking behaviours in these groups.

I examine the capacity and extent of local resource tracking by bellbirds/korimako (*Anthornis melanura*) on the Port Hills of Christchurch, New Zealand. Bellbirds are endemic honeyeaters (Meliphagidae), and, as such, are morphologically specialised for nectar feeding (Heather & Robertson 2015). Resource tracking is common among nectarivores because resources are typically patchily distributed and ephemeral in nature (Franklin & Noske 1999; Cotton 2004; Bennet et al. 2014; Kuiper et al. 2015). Bellbirds are facultative consumers; though they have an affinity for nectar they are highly versatile in their feeding behaviour and will consume fruit and invertebrates when nectar is unavailable (Gravatt 1971; Spurr et al. 2011). As facultative consumers, bellbirds are not limited by nectar availability, however, reports of non-random exploitation of some nectar resources (Spurr et al. 2011) and long distance nectar foraging movements (Spurr et al. 2010), may indicate that resource tracking is still of value to this species.

The potential for resource tracking by bellbirds, though they are generally highly mobile, may be restricted by behavioural processes including territoriality and competition (Bennet et al. 2014). These processes are expected to be particularly prevalent during the breeding season, which extends from October – January, when birds are more territorial (Craig & Douglas 1986; Anderson & Craig 2003). The Port Hills population is likely to experience less mobility constraints than in other New Zealand regions. Bellbirds in the area are widespread due to prolonged predator control efforts (Spurr et al. 2014), but exist at relatively low densities compared with some other regions and offshore islands (Sagar 1985; Anderson & Craig 2003; Spurr et al. 2010; Spurr et al. 2014). Local birds occupy large overlapping home ranges (c. 3.7ha), even during the breeding season (Spurr et al. 2010). Tūī, a dominant competitor elsewhere, are also largely absent from the Canterbury environment.

Resource tracking was assessed with regard to both spatial and temporal fluctuations in local nectar availability. Due to their affinity for nectar and documented non-random foraging movements, I expected bellbirds to be sensitive to the spatial distribution of nectar at local scales provided their mobility was not constrained by behavioural factors. As facultative consumers it may be reasonable to expect that bellbird tracking is sensitive to motivational variation; I therefore examined plant species consumption patterns independently of one another.

Tracking nectar availability through time typically requires movement of individuals over large spatial scales (i.e. between patches or fragments). Given that bellbirds are able to switch to alternative resources, such as honeydew, fruit and insects (Gravatt 1971); I expected that local bellbird populations would not be sensitive to short-term fluctuations in nectar supply within the flowering season. On the basis of previous studies, which have suggested that seasonal variation in floral abundance on the Port Hills (Spurr et al. 2011) may be linked with population changes over an annual scale (Spurr et al. 2014), I expected that bellbird populations would be sensitive to large-scale fluctuations in nectar availability, despite their dietary flexibility. In this study, I will quantify the

strength of the relationship between resource variation and population abundance at both an annual, and within season scale.

Hypotheses:

1. I expect that floral availability within 20 x 20m grid cells will be positively correlated with bellbird nectivory within 1 ha blocks. This will indicate that bellbirds are capable of spatially tracking floral resources at a local scale.

2. I further expect that the correlation between availability and consumption will be more consistent for ornithophilous nectar plant species than for entomophilous nectar plant species. This will demonstrate a higher motivation to track more valuable resources.

3. I expect that monthly variation in floral availability will not be correlated with variation in bellbird abundance within the flowering season. Diet switching should allow the local bellbird population to be immune to small fluctuations in nectar availability.

4. On the basis of previous work by Spurr (2011, 2014), I expect that bellbird abundance will be correlated with annual patterns of floral availability. Such a temporal pattern may be indicative of large scale spatial tracking, but may also be linked to greater dispersal at the end of breeding season.

2.3 Methodology

This study was conducted in two west-facing reserves of mixed hardwood-podocarp forest, c. 5 km apart, on the Port Hills, Christchurch: Kennedys Bush Reserve (135ha) (42.63'S, 172.62'E) and Omahu Bush Reserve (103ha) (43.66'S, 172.62'E). Observations of nectarivore activity and floral availability were made within a 1 ha plot measuring 100 m by 100 m at each site. Plots were representative of surrounding forest composition and were chosen on the basis of accessibility to ensure that each site could be adequately surveyed. Plots were subdivided into 25 grid cells, each measuring 20m by

20m. Data collection occurred from June 2015 until May 2016. Kennedys Bush was always monitored in the first week of each month while Omahu Bush was studied in the third.

2.3.1 Data collection

Bellbird activity and abundance data

Each month the grid was systematically traversed from a random starting cell to determine the activity of bellbirds within the plot. The observer spent a total of 5 minutes in each of the 25 cells, and all 25 cells were completed in one day. During this time the minimum number of individuals present within a cell (minimum count) and number of them that engaged in nectivorous activity was recorded. Minimum count is an abundance measure which describes the maximum number of individuals observed at any given time during the observation window. Minimum counts are conservative estimates but eliminate the potential for double counting within a single cell. Forest stands were of similar age and density and visibility did not vary markedly between cells or sites. Nectivorous events were defined as any visit by a bird in which the bird inserted its bill into the flower corolla. The plant species of all nectivorous events was noted. Flyovers were not included in cell counts. Cell observations commenced 1.5 hours after sunrise to minimise diel effects associated with the dawn chorus. Activity data was only collected on fine weather days to mitigate the effect of weather events. The day after activity observations were made, two 100 m x 20 m transects within the grid were monitored to assess overall abundance of bellbirds within the plot. Each transect was traversed over a 20 minute period and the number of bellbirds encountered within the transect was recorded. The first transect was carried out 1.5 hours after sunrise and the second transect was carried out an hour later.

Floral availability

Floral availability was used as a proxy for nectar availability due to the height of the canopy which made nectar measurement difficult. Floral availability within each cell was assessed with regard to the main nectar resources for bellbirds in the Port Hills area: fuchsia (*Fuchsia excorticata*), kowhai (*Sophora microphylla*), five-finger (*Pseudopanax arboreus*), and flax (*Phormium* spp.) (Spurr et al. 2011). Although bellbirds also feed on other species, such as *Cordyline australis* or *Pseudopanax crassifolius*, these species typically constitute less than 5% of the nectar diet of local bellbirds (Spurr et al. 2011). The cell location, DBH and the proportion of flowers open (1= 0-25%, 2= 26-50%, 3= 51-75%, 4= 76-100%) was recorded for every flowering tree within the plot each month. The proportion of flowers open was assessed relative to the expected maximum based on the presence of buds and immature flowers (Spurr et al. 2011). Binoculars were used in some cases to improve accuracy. Phenological data was collected immediately after the bird activity observations had been completed, although sometimes the assessment took multiple days (maximum three days) to complete. Additional measures, such as canopy diameter, and number of flowers, were not estimated due to the limited time frame in which floral availability could be surveyed each month.

2.3.2 Statistical analysis

Data processing

All flowering plants within a plot were assigned an index value based on their size (DBH) relative to the largest individual of that species within the plot and the floral openness score [$Availability\ score = \frac{ax}{b}cx$] (ax = DBH of individual, b = DBH of largest individual, cx= proportion of flowers available on individual). For flax species, the number of flowering stalks was used as a surrogate for DBH. These values were combined into measures of individual species floral availability and combined floral availability for each cell. Floral availability of all cells was combined to provide a measure of total floral availability for the month. Combined floral availability did not account for

interspecific variation in nectar production, which is a common issue in studies that calculate overall resource availability. All floral availability data was log (+1) transformed. Bellbird activity was also calculated at a cellular level for each month. The total number of individuals present and the total number of individuals engaging in nectivory of each plant species was calculated for each cell. Cell activity data was translated into a proportion of total activity for that month and arcsine square root transformed. Bird abundance data from the two transect lines were averaged to give an indication of overall bellbird abundance for each month. This data was square root transformed. Analysis was conducted using R, version 3.5.1. (R Development Core Team 2018).

Spatial tracking

Spatial autocorrelograms were produced for all cell-level response variables (e.g. floral availability, bird presence and nectivory) to evaluate patterns of spatial autocorrelation within the plot (Legendre & Legendre 1998). Mantel cross-correlograms were produced to examine the spatial overlap between these response variables. Correlograms assess the significance of autocorrelation (autocorrelograms) or correlation between distributions (cross-correlograms) at successive lag intervals so that the spatial extent of the trends could be quantified. Autocorrelograms and cross-correlograms considered two lag intervals of 20 m (cell width); a lag of 0 means within-cell correlations, while a lag of one indicates correlations among immediately adjacent cells. Pearson's correlation coefficient was used to test the significance of cross-correlations within individual cells (lag = 0). Significance was assessed from 1000 random permutations and a progressive Bonferroni correction was applied for multiple testing (Legendre & Legendre 1998).

Temporal tracking

Autoregressive integrated moving average (ARIMA) models, which account for temporal autocorrelation in time series data, were generated for each site using the monthly bird abundance data. The Box-Ljung Q statistic was then produced to assess autocorrelation between months. As

autocorrelation was not found to be present, OLS regression models were produced to determine the temporal relationship between monthly combined floral availability and bird abundance for each site. The temporal relationship was assessed at two scales: within the flowering period, and over the entire annual period.

2.4 Results

2.4.1 Site composition

A total of 203 nectivory events were recorded for bellbirds. Nectar was taken from eight plant species: fuchsia, kowhai, five finger, whararikí, harakeke, lancewood, lemonwood, and the New Zealand jasmine (*Parsonsia heterophylla*). Four focal plant species, fuchsia, kowhai, five finger and flax (*Phormium* spp.), accounted for most of these nectivorous events (98%). All focal species were present at the Kennedys Bush site () but only five finger and fuchsia were present at the Omahu Bush site (). The absence of *Phormium* species in Omahu Bush meant that the nectar feeding season spanned from June to December, whereas in Kennedys Bush nectivory continued until February. Peak productivity of nectar producing species is staggered throughout the flowering season. Five finger reaches peak productivity in late August – early September, kowhai in October, fuchsia in November, whararikí (*Phormium cooki*anum) in December and harakeke (*Phormium tenax*) in January (;).

At Kennedys Bush flowering was confined to small discrete patches as suggested by low levels of autocorrelation. Only the January trial indicated significant autocorrelation of floral resources where *Phormium* spp. were positively autocorrelated within the first lag class ($r = 0.37$, $p = 0.009$). Flowering in Omahu Bush occurred in larger patches with higher rates of autocorrelation between cells. Five finger displayed significant autocorrelation at the first lag class in June ($r = 0.34$, $p = 0.002$), July ($r = 0.35$, $p = 0.004$) and August ($r = 0.37$, $p = 0.001$). Fuchsia was autocorrelated at the first lag class in October ($r = 0.39$, $p = 0.001$), November ($r = 0.034$, $p = 0.004$) and December ($r = 0.28$, $p =$

0.017). Bellbird response variables (nectivory and presence) did not suggest significant autocorrelation at a cell level in any month at either site.

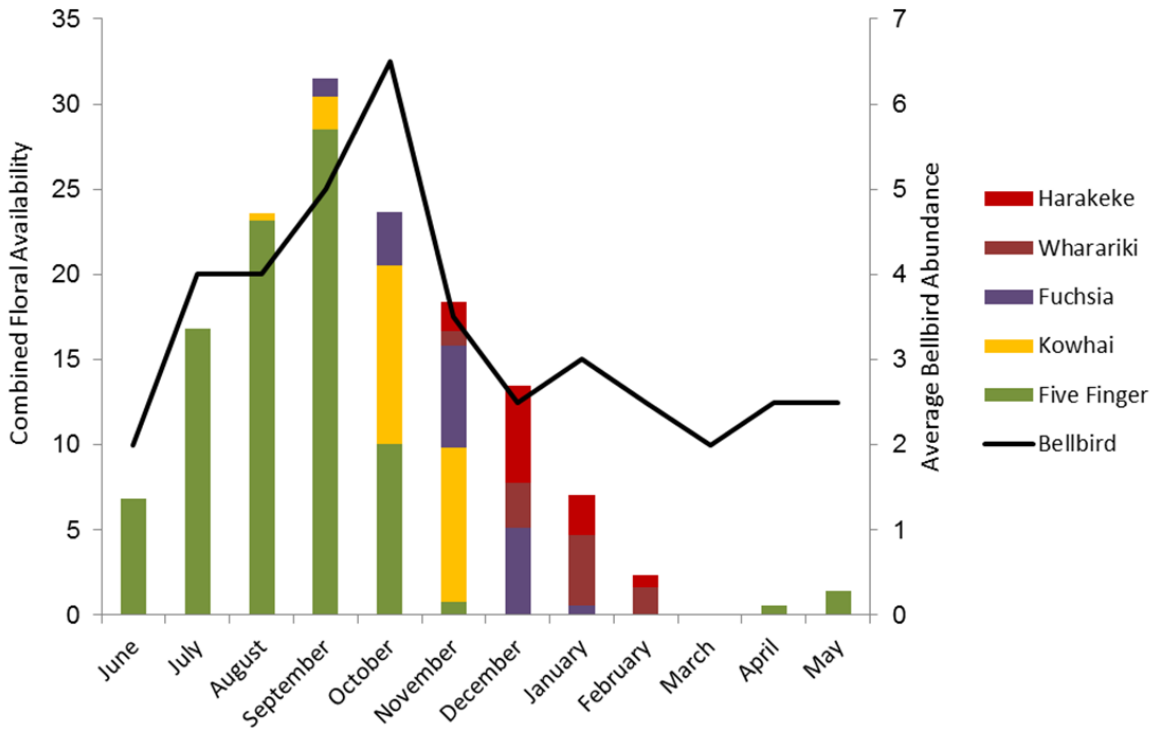

Figure 1: Floral availability and bellbird abundance at Kennedys Bush. Floral availability is the combined scores of all flowering plants within the observation plot. Bellbird abundance is the mean of the two 100 m x 20 m transect counts, and is expected to be an index of the true count of bellbirds within the full 100 m x 100 m plot.

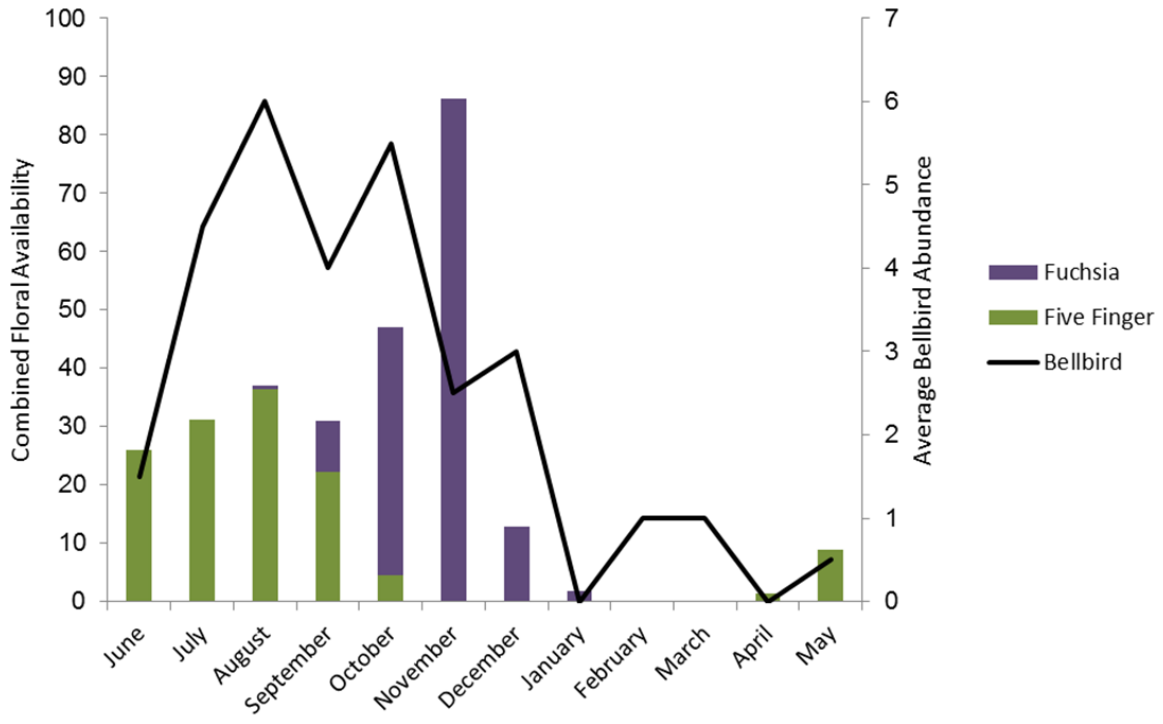

Figure 2: Floral availability and bellbird abundance at Omahu Bush. Floral availability is the combined scores of all flowering plants within the observation plot. Bellbird abundance is the mean of the two 100 m x 20 m transect counts, and is expected to be an index of the true count of bellbirds within the full 100 m x 100 m plot.

2.4.2 Spatial resource tracking

Species level response

Five Finger

Five finger was the most numerically dominant of the focal species present within the plot at Kennedys Bush (123 flowering individuals at peak). Nectar was consumed between the months of June and October and was the main source of nectar from June through to September. Five finger nectivory by bellbirds was significantly correlated with five finger floral availability within the

20x20m cells (lag 0) in August ($r = 0.49$, $p = 0.013$), September ($r = 0.76$, $p < 0.0005$) and October ($r = 0.47$, $p = 0.018$).

The Omahu Bush site contained 189 flowering five finger individuals at peak. The nectar was consumed from June until September and was the main source of nectar for bellbirds from June through to August. Bellbird nectivory was significantly correlated at a cell level in August only ($r = 0.46$, $p = 0.019$), which was also the month of peak production. The correlations were significant when considered at the first lag distance class for both July ($r = 0.21$, $p = 0.018$) and August ($r = 0.33$, $p = 0.0009$).

Kowhai

Kowhai was only present within the Kennedys Bush site (52 individuals). Nectar was consumed between August and November. It was the main source of nectar for foraging bellbirds in October. Cross correlation could not be examined in August as only one cell contained flowering individuals. Bellbird nectivory and floral availability were correlated at a cell level in September ($r = 0.73$, $p < 0.0005$), October ($r = 0.57$, $p = 0.002$) and November ($r = 0.72$, $P < 0.0005$).

Fuchsia

Fuchsia was present in relatively similar numbers to kowhai within the Kennedys Bush plot (47 individuals). It was consumed from October until December, and was the main source of nectar for bellbirds in November and December. The correlation between bellbird nectivory and floral availability was significant at a cell level only for all months of consumption (October; $r = 0.76$, $p < 0.0005$, November; $r = 0.85$, $p < 0.0005$, December; $r = 0.59$, $p = 0.0018$).

Omahu Bush had a much larger fuchsia population (356 individuals flowering at peak). It was consumed between September and December and was the main source of nectar for bellbirds throughout this period. Despite being present in larger patches than Kennedys Bush, bellbird nectivory and floral availability were still only correlated at a within cell level during the months of

consumption (September; r = 0.5, p = 0.009, October; r = 0.43, p = 0.03, November; r = 0.49, p = 0.012, December; r = 0.54, p = 0.005).

Flax

Phormium species were only present in Kennedys Bush. Two species, harakeke (*Phormium tenax*) and whaririki (*Phormium cookianum*) both flowered in relatively low numbers at the site from November until February (). Harakeke was consumed by bellbirds between December and February, while whaririki was consumed from November until January. Visitation was too low to perform cross-correlation either side of peak flowering. In all of these cases nectivory was only detected in the most productive cell. During peak flowering (whaririki - December, harakeke – January) there was a significant correlation between nectivory and floral availability within the study cells (whaririki; r = 0.84, p <0.0005, harakeke; r = 0.9, p < 0.0005). Harakeke was also correlated at a lag distance of 1 cell, but the strength of the correlation was less (r=0.30, p = 0.009).

Combined spatial response

In Kennedys Bush, combined floral availability (all plant species) was significantly and positively correlated with bellbird presence within the 20 x 20 m cells (lag = 0) in August, September, November, December and January but not June, July or October (Table 1). In Omahu Bush, bellbird presence was significantly and positively correlated with floral availability for October, November, and December (Table 1). Bellbird presence was also correlated at the first lag class in August (Table 1).

In all cases where fuchsia, kowhai, and flax were numerically dominant, an overall correlation between bellbird presence and combined floral availability was observed (November – February in Kennedys Bush and October – December in Omahu Bush). Inconsistent overall patterns were observed where five-finger was numerically dominant (June – October in Kennedys Bush, June-September in Omahu Bush). In cases where five finger was numerically dominant, and the main

source of nectar for foraging birds, some degree of overall resource tracking was observed, especially during peak production (Kennedys – August and September, Omahu – August; Table 1). Where five finger was numerically dominant, but consumed at lower frequencies than other nectar producing species (Kennedys Bush: October, Omahu Bush: September; Table 1), there was no evidence of overall resource tracking.

Table 1: Cross correlation of combined floral availability and bellbird presence. Only the first lag interval is shown as all of the correlograms were significant beyond this distance. Significance of the correlations (r) is indicated by the p value (P). Values indicated by * were significant after progressive Bonferroni correction.

	Kennedys Bush				Omahu Bush			
	Lag 0		Lag 1		Lag 0		Lag 1	
	r	P	r	P	r	P	r	P
June	0.08	0.720	0.12	0.302	0.34	0.086	0.21	0.279
July	0.32	0.121	0.17	0.208	0.13	0.542	0.17	0.062
August	0.40	**0.048***	-0.06	0.489	0.34	0.096	0.23	**0.018***
September	0.45	**0.024***	0.13	0.267	0.39	0.053	-0.02	0.461
October	0.36	0.082	-0.14	0.295	0.47	**0.018***	0.12	0.123
November	0.49	**0.013***	0.08	0.317	0.49	**0.012***	0.17	0.066
December	0.51	**0.008***	0.31	0.061	0.41	**0.041***	0.19	0.056
January	0.51	**0.009***	0.19	0.147	na	na	na	na

2.4.3 Temporal resource tracking

Monthly bellbird abundance was significantly correlated with total floral availability at both sites when examined over an annual period (Omahu Bush; $F_{1,10} = 16.02$, $p = 0.025$, ; Kennedys Bush $F_{1,10} = 8.5$, $p = 0.015$,). The relationship was insignificant in both cases when examined within the period of nectar consumption only (Omahu Bush; $F_{1,6} = 1.99$, $p = 0.317$; Kennedys Bush $F_{1,7} = 3.17$, $p = 0.118$).

2.5 Discussion

2.5.1 Spatial resource tracking

Bellbirds were able to track changes in the spatial distribution of floral resources at a local (1 ha) scale within native bush remnants. The extent of resource tracking observed each month appears to have been influenced by individual plant characteristics. The distributions of fuchsia, kowhai and flax were tracked in every month that they were consumed at both sites, while five finger was only tracked in a subset of months in which it was consumed. This disparity likely related to the pollination syndrome, and associated value, of the plants in question.

Fuchsia, kowhai and flax are ornithophilous species which bear large, nectar rich flowers (Godley 1979; Appendix A). Five finger, despite being an important part of the bellbird nectar diet (Spurr et al. 2011), is typical of the entomophilous syndrome and produces clusters of smaller, less rewarding flowers (Godley 1979; Castro & Robertson 1997). The ornithophilous flowers consistently offer greater energetic rewards per flower which may result in a higher motivation to track these species relative to the associated cost (Blendinger et al. 2015; Fowler et al. 2016). Five finger was tracked to a greater extent at Kennedys Bush, where it was available in smaller patches and alternative resources were not as readily available. Conditional tracking with respect to this species seems to indicate that failure to track five finger in other months is tied to lack of motivation rather than lack

of capacity to do so. Motivational disparities may also exist between ornithophilous species in response to variation in nectar production, or floral strategy (Appendix A). A limitation of this study is that, due to time and resource constraints, only two plots could be examined. Greater replication would allow variation between ornithophilous species to be examined. Data from smaller spatial scales, e.g. tree level, would also allow the most important resource characteristics to be identified (Stewart & Dudash 2017; Appendix A).

Foraging decisions made by facultative consumers are less constrained and, therefore, likely to be more flexible than decisions made by obligate, or highly specialist consumers (Cotton 2007; Hamilton et al. 2017). This research demonstrates that in addition to flexible investment with respect to resource quality, the tracking response could be flexible over a single plant species. Five finger was tracked differently between sites and between months. Several factors may have contributed to the variable motivation to track this resource, including resource availability, patch size, quality of alternative resources, and forager energetic requirements. Most research on spatial resource tracking by facultative nectarivores, such as sunbirds or honeyeaters, has examined tracking of a single, high value, monodominant species, such as Aloe, Protea or Eucalypt (Symes et al. 2008; Hall et al. 2011; Bennet et al. 2014; Kuiper et al. 2015; Schmid et al. 2015). The responses reported in these studies, both strong (Kuiper et al. 2015), and weak (Hall et al. 2011), may also be flexible on the basis of motivation. External factors that could affect tracking motivation include modification to habitat structure or composition (Telleria & Perez-Tris 2006), fragmentation of resource patches (Lehouck et al. 2009), and climate driven changes to nectar availability (Bennet et al. 2014).

The overall distribution of bellbirds was correlated with the combined distribution of floral resources in a subset of months at each site. In Kennedys Bush, where all flowering species were present in small discrete patches (smaller than the 20 x 20 m grid cell size), bellbird presence was correlated at a cell level with overall floral availability in August, September, November, December and January. In

Omahu Bush, where the floral community was denser but less diverse, bellbird presence was correlated at a cell level in October, November and December and at a greater distance in August. Flexibility of tracking response in relation to resource value may largely explain the observed discrepancies between sites, despite differences in composition. Bellbirds tracked the overall distribution of resources in ornithophilous-flowering dominant months, but were inconsistent in their tracking response in entomophilous-flowering dominant months. High value, ornithophilous species appear to have a disproportionate effect on tracking response relative to their abundance during these entomophilous dominant months. This finding highlights the issues of using combined measures that do not account for species-level variation to examine resource tracking responses. A combined availability approach has been widely adopted in previous research, both for nectarivores (Pyke 1981; Malizia 2000; Cotton 2007; Jiménez et al. 2012) and frugivores (Sacarro et al. 2004; Telleria & Perez-Tris 2007; Guitian & Munilla 2009).

Ignoring variation in consumer preference may result in a failure to identify resource tracking processes. As is the case in this study, spatial tracking of specific resources can be masked by the availability of abundant but less important resources. Franklin & Noske (1999) examined resource tracking at three spatio-temporal scales by five avian nectarivores, the highly nectar dependant rainbow lorikeet, and four honeyeater species (little friarbirds, brown honeyeaters, silver-crowned friarbird, yellow-throated miner) that consume nectar on a facultative basis. Though nectar availability data was collected separately for all major flowering species, only combined measures of nectar-standing crop were used to quantify resource tracking. Of the five nectarivore species examined, only the rainbow lorikeet and one honeyeater species, the little friarbird, tracked nectar availability at any of the studied scales (Franklin & Noske 1999). While the weak tracking response may be explained by behavioural constraints in some cases, brown honeyeaters' dispersion was correlated with floral and habitat structure (Franklin & Noske 1999). This may suggest that selective resource tracking was occurring, but was masked by the measure of availability used. Several other studies of facultative consumers have noted weaker or less conclusive tracking responses than

anticipated when using combined resource descriptors (Pyke 1981; Malizia et al. 2000; Hawkins 2004; Carnicer et al. 2009). Selective tracking may be worth examining in these instances.

The results of this trial represent a local environment that is largely free of behavioural constraints on motility. Bellbirds on the Christchurch Port Hills occur at lower densities, and occupy larger home ranges than many island-based bellbird populations (Sagar 1985; Anderson & Craig 2003; Spurr et al. 2010). Port Hill bellbirds also do not experience competitive exclusion by the more dominant tūī (Rasch & Craig 1988). While spatial resource tracking in this trial was possible due to the motility of resident birds, in environments where motility is restricted by interspecific and intraspecific competition, tracking may not occur to the same extent (Bennet et al. 2014). In cases where motility is restricted, resource tracking may still occur, but at smaller spatial scales, e.g. within individual home ranges or within single trees.

2.5.2 Temporal resource tracking

Bellbird populations at both research sites exhibited crude temporal tracking. Populations did not respond to fluctuations in nectar availability within the flowering period. Increased intake of fruit or invertebrates likely insulated them from resource fluctuations during this period (Gravatt 1971; Gleditsch et al. 2017). Temporal tracking at a within-season scale may have indicated that local birds were moving within and between bush fragments in order to exploit the most profitable native resource patches at any given time. Bellbirds may not have been motivated to track resources at these larger spatial scales due to the elevated cost of movement. Behavioural constraints may also have limited motility at these larger scales. Spurr et al. (2010) radio tracked Kennedys Bush bellbirds during their breeding season and determined that individual birds moved a maximum distance of 500m. This level of motility may not have allowed individuals to experience and exploit sufficient variation in nectar availability to warrant patch scale resource tracking.

Given that spatial resource tracking was determined to be plant specific at a local scale, it is possible that within-season temporal movements were also influenced by plant specific variables. Spurr et al. (2010) noted that kowhai and flax are concentrated in gullies and at forest edges within Kennedys Bush. Large scale spatiotemporal tracking of species with a clumped distribution may be more beneficial than tracking species which are more uniformly distributed within the reserves. Species specific temporal responses could be evaluated by examining spatial trends over larger scales.

Temporal correlation between bellbird abundance and resource availability was observed at an annual scale. Bellbird abundance decreased when nectar resources were no longer available within the reserves. This finding confirms a match between previously reported trends in nectar availability (Spurr et al. 2011) and population abundance (Spurr et al. 2014) in native bush fragments on the Port Hills. It is, however, in contrast with two prior studies. Gravatt (1970) and Spurr et al. (1992) monitored honeyeater populations over an annual period on Little Barrier Island and North Okarito respectively. Both found that while tūī populations fluctuated in response to flowering cycles, bellbird populations did not. This suggests that the seasonal tracking response in bellbirds may be site dependent. For example, nectar supply on Little Barrier Island is more continuous than on the Port Hills due to higher resource diversity (Gravatt 1970). Continuous supply on Little Barrier Island over an annual period may mean foraging patterns there are more comparable to the 'within flowering period' temporal response of Port Hill bellbirds.

The annual tracking pattern observed in this study is characterised by a single large exodus. One explanation for the observed population decline is regional scale tracking of floral resources. Earlier studies have hypothesised that non-breeding bellbirds leave the native nectar dominated Port Hills reserves in autumn and winter in order to exploit adventive nectar sources in the nearby Christchurch city (Medway 2011; Spurr et al. 2011; Spurr et al. 2014). As the local population decline coincides with the end of the breeding period, an alternative explanation for the seasonal trend is of greater motility outside of the breeding season and natal dispersal. Movements into the city of

Christchurch need to be characterised in greater detail to determine if the seasonal decline is driven by temporal changes in resource supply or whether it is an artefact of behavioural changes.

2.6 Conclusion

Bellbirds responded to spatial and temporal shifts in nectar distribution within native bush fragments on the Port Hills. Tracking appears to have been more sensitive to spatial variability in resources at a 1ha scale than to temporal variability, as only crude seasonal level temporal tracking was observed. Examining spatial responses at an individual plant-species level allowed examination of motivational constraints on tracking. It was determined that bellbirds were flexible in their tracking response, likely investing more effort into tracking high value, ornithophilous resources. The presence of a value-dependent flexible tracking response is likely a feature of many facultative consumers and requires further investigation in other systems. Future work on facultative nectarivores should avoid combined measures of resource availability and instead focus on grouping resources by value, e.g. syndrome or floral production strategy (Stewart & Dudash 2017), or on tracking of key high value resources (Symes et al. 2008; Kuiper et al. 2015).

Understanding how species respond to variation in resources across different spatial scales can have important ecological implications. Bellbird ability to track key nectar resources at a local scale observed in this study may assist in the maintenance of key mutualisms, and facilitate persistence in patchy, low quality environments. In this system mobility does not appear to have constrained tracking movements; spatial resource tracking occurred throughout the breeding season in both sites. In other systems, where bellbirds exist at higher densities, or alongside tūī, the expression of resource tracking may be reduced by greater limitations on mobility (Bennet et al. 2014). In systems with high levels of interference resource tracking may still be facilitated at this scale by spatial or temporal partitioning of resources (Craig & Douglas 1984; Craig & Douglas 1986).

Chapter 3

Use of fine scale song dialects to characterise seasonal movements of Port Hills bellbirds (*Anthornis melanura*)

3.1 Abstract

Bellbirds from the Port Hills undergo seasonal dispersal into urban environments. It has previously been suggested that these movements are driven by flowering of exotic nectar sources within the city. A song type matching technique was used to characterise the nature of dispersal behaviour. Male bellbird vocalisations were recorded at 29 sites on the Port Hills. Melody calls were extracted and manually classified into groups based on visual inspection of spectrograms and was blind with respect to location. Three geographically distinct dialect groups were apparent in source population recordings. Urban recording was conducted following seasonal dispersal. Port Hills dialects were detected at 22 urban sites in the greater Christchurch region. In 84% of cases the urban song types matched the dialect of the closest potential source population. Proximity appears to be the biggest driver of this dispersal behaviour. The observed movement pattern suggests that if large scale resource tracking is occurring, it is occurring at patch scale within the birds expanded range rather than at a landscape level. The results of this study may also indicate that dispersal movements by male bellbirds are more distance limited than previously assumed.

3.2 Introduction

Bellbirds (*Anthornis melanura*) are widespread throughout much of New Zealand's South Island, including many urban centres, such as Dunedin and Nelson (Spurr 2012; Heather & Robertson 2015). A notable exception is urban Christchurch City, where bellbirds are mostly rare and seasonally transient (Spurr et al. 2014). The native forests of the Port Hills, which flank Christchurch to the

south-west, act as an important source population for these transient birds (Spurr et al. 2014). Bellbirds are present in relatively high numbers within forest fragments on the Port Hills throughout the year (Spurr et al. 2014). During late autumn, winter, and early spring, some individuals disperse into the city and other surrounding urban areas, where they reside in small bush patches and domestic gardens (Spurr et al. 2014). These individuals remain in Christchurch until the following breeding season (late spring–summer), at which point they return to forest fragments in the Port Hills (Spurr et al. 2014).

It has been suggested that seasonal movements by Port Hills bellbirds may be in response to landscape scale changes in resource availability (Spurr et al. 2011). Bellbirds have a varied diet, but preferentially consume nectar when it is available (Gravatt 1970; Spurr et al. 2011). Nectar resources are scarce in Port Hills reserves during autumn and winter because bush remnants are largely composed of native species, few of which flower in these months (Spurr et al. 2011; Chapter 2). The urban gardens of Christchurch city, however, contain large numbers of winter-flowering adventive species (e.g. *Banksia, Protea, Camellia, Corymbia, Eucalyptus, Grevillea,* and *Callistemon*) that could provide an alternative source of high quality nectar at this time (Spurr et al. 2014). Dispersal in response to shifts in the distribution of nectar between the Port Hills and Christchurch (Spurr et al. 2011) would be indicative of large scale resource tracking (García & Ortiz-Pulido 2004; Kuiper et al. 2015). As bellbirds have already been shown to track spatial variation in nectar availability at a local scale (Chapter 2), the ability to respond to patchiness at this larger scale would suggest that the tracking response is not confined to local scale-specific mechanisms, or that local scale mechanisms operate over larger scales when birds are more mobile (García & Ortiz-Pulido 2004).

In order to determine whether the seasonal movements of bellbirds are driven by resource tracking processes, it is necessary to characterise their movements in greater detail. Radio telemetry has been suggested as a means to examine seasonal movements of individuals (Spurr et al. 2010). Banding of individuals in source population sites could also allow for quantification of individual

movements. Neither of these techniques is likely to be feasible for examining trends at a population level, due to the high cost and difficulty associated with targeting sufficient numbers of dispersing individuals. In this study, I examine the feasibility of an alternative, population targeted technique, the use of song type, to quantify seasonal movements of Port Hills bellbirds.

Bellbird repertoires include a variety of song types, some of which vary geographically and form dialectal groups (Brunton & Li 2006; Brunton et al. 2008a). Dialectal songs are those that are unique to a geographical area, arising as a result of inaccurate song transmission between generations, e.g. copying errors (Baker & Cunningham 1985; Kroodsma 2004). In many cases singing the local song has adaptive value for individual birds, for example it may be easier to hold a territory (Osiejuk et al. 2007), or attract a mate (Rowe & Bell 2007). When dialects serve an adaptive purpose, groupings may be stable over long temporal periods (Baker & Cunningham 1985; Kroodsma 2004; Wright *et al.* 2008). Dialectal songs have been reported in several other New Zealand songbird species in addition to the bellbird, including kōkako (*Callaeas cinerea wilsoni*; Bradley et al. 2012), tūī (*Prosthemadera novaeseelandiae*; Hill 2013), and North Island saddleback (*Philesturnus carunculatus*; Jenkins 1978).

The presence of a geographically stereotyped song type is useful as a means to study both dispersal and population dynamics (MacDougall-Shackleton et al. 2002; Anderson et al. 2005), and as a conservation tool, e.g. post translocation anchoring (Molles et al. 2008). Brunton et al. (2008a) has previously used geographic variation in bellbird song type to determine the likely source population of a newly established population at Tawharanui. Tawharanui is a coastal headland situated equal distances (c. 20 km) from two large bellbird populations on Little Barrier Island and Tiritiri Mātangi. Recordings from Tawharanui bellbirds were visually matched to song types found on Little Barrier Island but not those found on Tiritiri Mātangi, indicating Little Barrier Island was the most likely source population (Brunton et al. 2008a). Bellbirds breed in Port Hills forest fragments of varying size, age, and degree of separation, and previous observations have suggested that song types vary from fragment to fragment. I developed a similar technique to that used by Brunton et al (2008a) to

determine whether variation in male song type across the Port Hills populations could be used to pinpoint the source locations of urban bellbirds, and characterise their dispersal patterns.

Hypotheses:

1. Male song types across populations in the Port Hills will form geographically distinct, dialectal groups.

2. Source populations (Port Hills) song types will be present in the Christchurch environment. This will indicate seasonal dispersal into Christchurch from Port Hills source populations.

3.3 Methodology

3.3.1 Data collection

Source population recording

Single channel, Department of Conservation recording devices were deployed across 29 sites on the Port Hills adjacent to Christchurch, spanning from Ahuriri Reserve in the west to Rapanui Reserve in the east (Appendix B). Recording sites were concentrated in areas of high bellbird abundance (e.g. Kennedys Bush, Sugarloaf, and Omahu Bush) but all accessible, substantial patches of native forest were sampled. Recorders were mounted on trees that were, where possible, >50 m from the forest edge, at a height of 2 m. Source population recording at these sites occurred between March and June of 2016. During deployment, the recorders were programmed to record continuously during daylight hours. Recording days per site ranged from 2–9 days due to variation in battery life. All recordings were digitised at a 16-bit precision with a sampling rate of 32 kHz and frequency range 0 - 16 kHz. Using a low sampling rate enabled longer recorder deployments, while still ensuring that the fundamental frequencies of bellbird notes would be captured to enable song-type identification.

Urban recording

Twenty five automated recording devices (single channel, Department of Conservation devices) were deployed in urban gardens and small forested reserves in Christchurch city and its satellite towns, e.g. Lincoln and Tai Tapu (Appendix C). As with source population recording, recorders were installed in small patches of vegetation and mounted to trees at a height of 2 m; recording was continuous during daylight hours. Urban recording were collected from July–September, 2016. In addition to the automated recordings; incidental recordings of bellbirds, made on handheld devices between 2014 and 2016 were included in the urban dataset, incidental recordings were made during the period of winter – early summer. Handheld devices used for incidental recordings included a SoundDevices 722 Hard Disk Field Recorder with Telinga Pro6 Twin Science microphone mounted in a parabola, a Tascam DR-40 linear PCM Recorder, and an iPhone 4s. Sampling rates varied across devices, but frequencies above 4500 Hz were ignored for analysis purposes.

3.3.2 Song analysis

Raw recordings were processed using Kaleidoscope Pro software (Wildlife Acoustics Inc., 2018). The parameters for signals of interest were set as: frequency of 1000–4200 Hz, total duration of 1.0–3.5 seconds and a maximum between-syllable gap of 0.35 seconds. The frequency window excluded harmonics, but high-frequency harmonics were not captured by the automated recorders, and are not required for basic song type classification. Spectrograms were generated for all resulting signals using a 512-sample Hann window (50% overlap) with a frequency resolution of 15.6 Hz. The subset of bellbird vocalisations of interest to this study were relatively long, stereotyped melodies, without repetitive elements, that were present at multiple recording locations. A wide variety of shorter, repetitive, and more variable vocalisations were also detected but were not included in this analysis. Bellbird vocalisations which met the search criteria were manually classified into groups of similar

vocalisations based on visual inspection of spectrograms. Classifications were blind with respect to location to avoid biasing resulting clusters.

Song types identified in this research are likely representative of male singers (Brunton & Li 2006). Brunton and Li (2006) found that female bellbirds did not have structurally distinct song types, instead song types were characterised by different combinations and repetitions of the same basic song units. Visual matching techniques employed in this study were more compatible with the structurally distinct song types of males which could be more easily stereotyped for comparison. Female bellbirds sing less frequently than males during the non-breeding season (when source population recording occurred) and were likely also under-represented in source population recordings (Brunton & Li 2006). Raw urban recordings were manually inspected, in addition to the Kaleidoscope filtering process, to increase the chances of detecting quiet or rare song signals against a greater background noise profile. Urban melodies were visually compared to the main song type groups identified from source Port Hills population recordings. The presence of a song type match was assumed to indicate the likely source population of the individual (Brunton et al. 2008a). Classifications of urban recordings were also performed blind with respect to location.

3.3.3 Statistical analysis

In order to determine whether song types were geographically distinct, a non-metric multidimensional scaling (NMDS) ordination analysis was performed to assess the similarity of source population sites on the basis of song type composition. NMDS is a form of ordination analysis that maximises rank-order correlation between distance measures and distance in ordination space. A permutational multivariate analysis of variance analogue, ADONIS, was conducted to examine the significance of longitude and latitude in partitioning the sites. These analyses were conducted using the statistical software R, version 3.5.1 (R Development Core Team 2018) and the ‘vegan’ analysis package.

To determine the geographical extent of each song type, sites were classified according to the most numerous song type present (dominant song type) and mapped using ArcGIS 10.3 (ERSI 2011). In cases where source song types were matched to urban recordings, a distance score (km) was calculated to define the minimum straight line distance to the closest possible source location of a matching dominant type. Straight-line distances between locations were estimated using Google Earth Pro software.

3.4 Results

3.4.1 Source population song types

Three major song types were identified during classification (Figure 3; Table 2). Each song type had two or three variants which deviated slightly from the most common form but retained the key characteristics of the type (Figure 3). At least one of the three identified song types was present in recordings from 26 of the source population sites; the only exceptions were Scotts Bush, Rapanui Bush and Jollies Bush (Table 2). No full songs were detected at Scotts Bush, and songs detected at Rapanui Bush Reserve or Jollies Bush reserve did not match the three main groups (Table 2). The majority of sites were represented by a single song type only (17/26) but secondary, less numerous types were detected at nine of the locations (Table 2). NMDS analysis confirmed that song type groups were spatially separated (Figure 4). Latitude and longitude were both significant predictors of site song type composition (longitude: $R^2 = 0.011$, $p = 0.0004$; latitude: $R^2 = 0.77$, $p = 0.0207$).

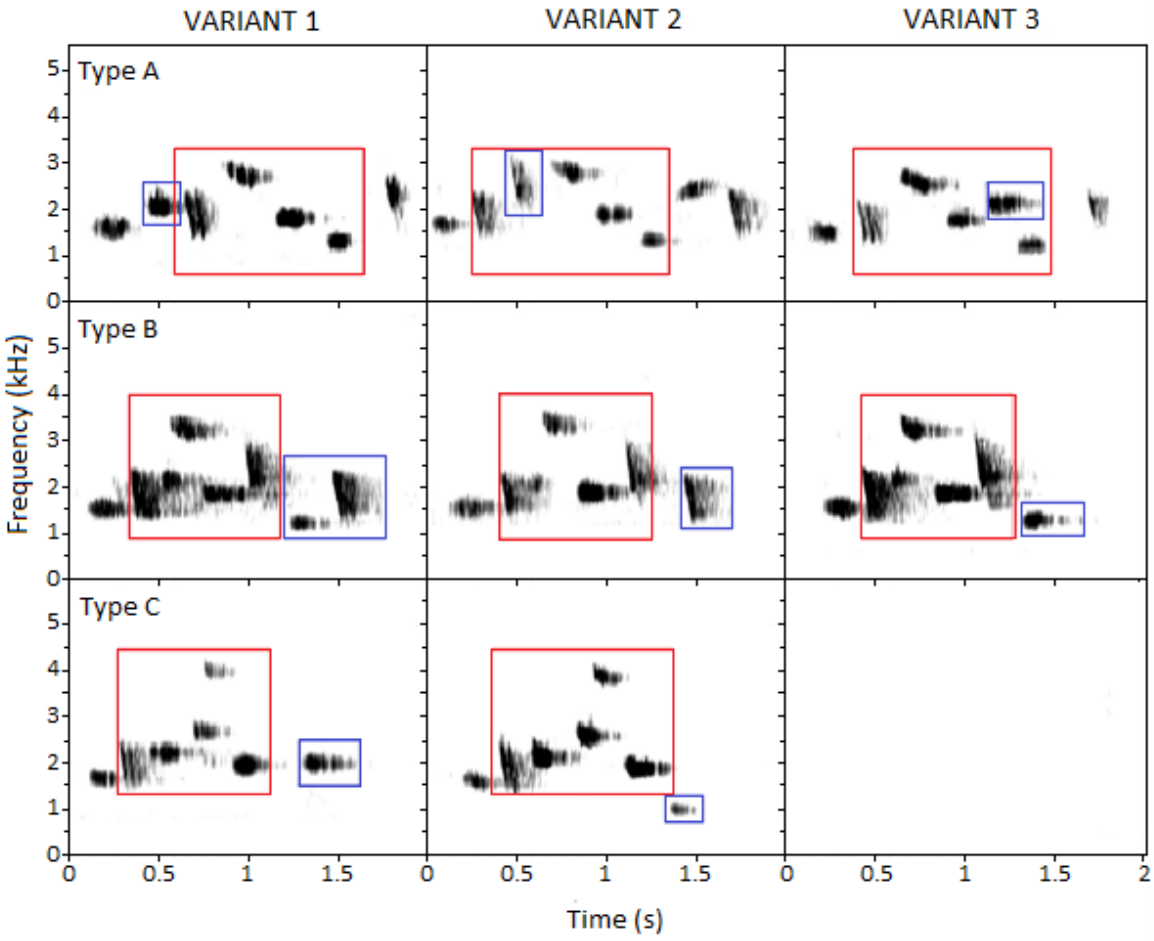

Figure 3: Example song types of each of the three main groups used in classification. Variants are listed by numerical dominance in the source population recordings. The red boxes indicate the main stereotyped sequence of each song type group. Blue boxes indicate points where variants differ from one another.

Table 2: Number of shared song types detected at each of the Port Hill recording sites.

Recorder Location	*Type A*	*Type B*	*Type C*	*Dominant Type*
Ahuriri	40	0	69	Type C
Omahu Bush Reserve 1	0	0	466	Type C
Omahu Bush Reserve 2	0	0	8	Type C
Omahu Bush Reserve 3	0	0	2	Type C
Omahu Bush Reserve 4	0	0	1	Type C
Living Springs	0	0	21	Type C
Cass Peak 1	1	0	2	Type C
Cass Peak 2	0	0	5	Type C
Kennedys Bush Reserve 1	0	1296	0	Type B
Kennedys Bush Reserve 2	1	31	0	Type B
Kennedys Bush Reserve 3	1	4	0	Type B
Kennedys Bush Reserve 4	1	13	0	Type B
Ohinetahi Bush Reserve 1	0	82	0	Type B
Ohinetahi Bush Reserve 2	0	70	0	Type B
Ohinetahi Bush Reserve 3	0	4	0	Type B
Worlsey Spur	1	3	0	Type B
Sugarloaf Scenic Reserve 1	119	17	0	Type A
Sugarloaf Scenic Reserve 2	275	0	0	Type A
Sugarloaf Scenic Reserve 3	771	1	0	Type A
Victoria Park	2	0	0	Type A
Bowenvale Recreation Reserve 1	72	0	0	Type A
Bowenvale Recreation Reserve 2	4	0	0	Type A
Bowenvale Recreation Reserve - Bush Head	8	0	0	Type A
Bowenvale Recreation Reserve - Scotts Reserve	0	0	0	No Melody Type
Rapaki Valley	1	0	0	Type A
Major Hornbrook Reserve	4	0	0	Type A
Jollies Bush Scenic Reserve	0	0	0	No Shared Type
Rapanui Reserve	0	0	0	No Shared Type

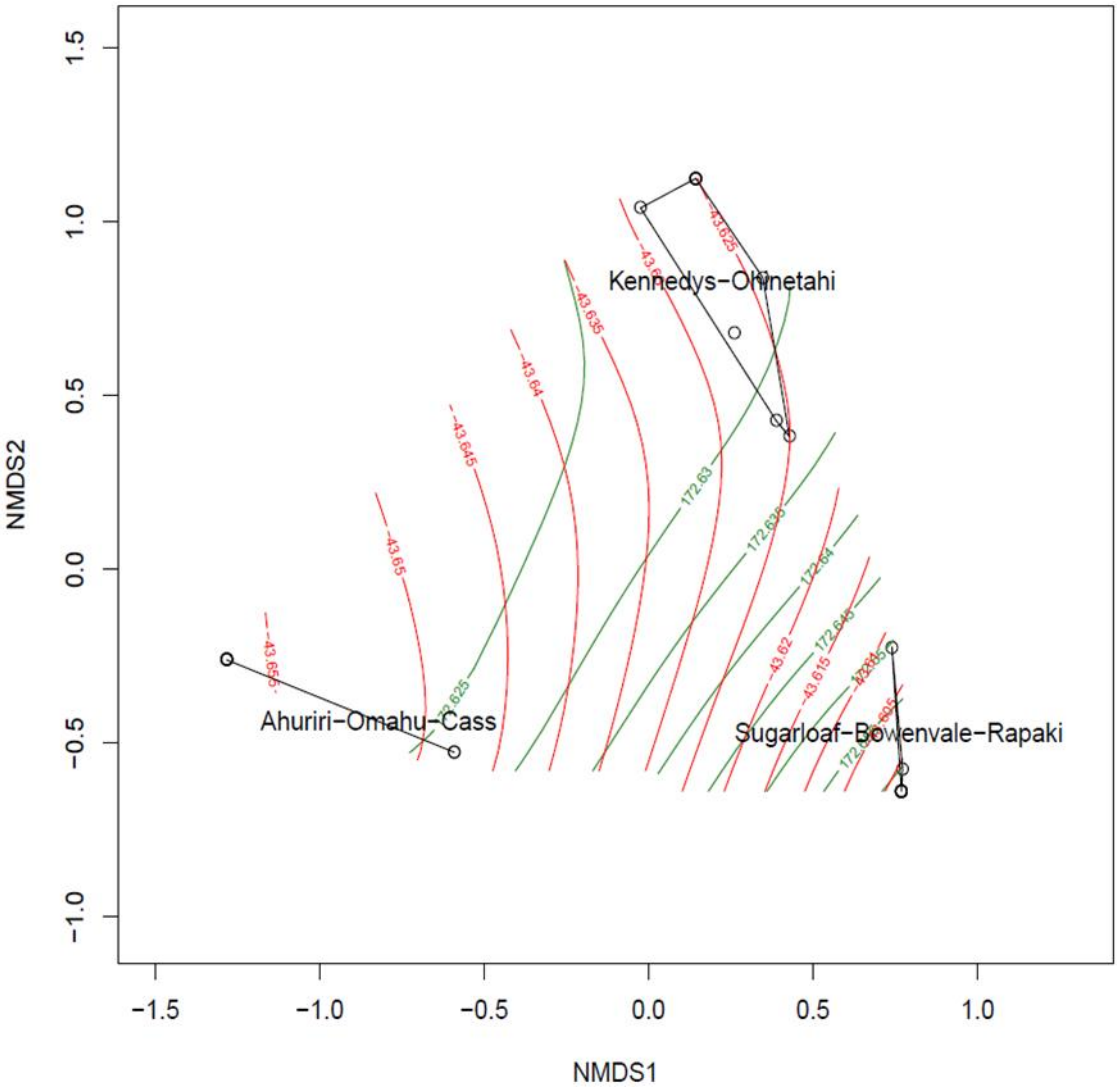

Figure 4: Non-metric multidimensional scaling plot displaying the similarities between labelled source population sites with respect to song type composition. Convex hulls show sites grouped by dominant song type. Isoclines show longitude and latitude.

Song Type A is the most eastern song type group; it was dominant at nine locations spanning a maximum distance of 6.9 km from Major Hornbrook Reserve in the east to Sugarloaf Scenic Reserve in the west (Figure 5). Song Type A was most numerous at a site in Sugarloaf Scenic Reserve (-43.604527, 172.651364).

Song Type B is the central song type group composed of nine recording sites over a maximum distance of 1.70 km (Figure 5). Song Type B was most numerous at the central Kennedys Bush Reserve site (-43.628794, 172.623266) but was also dominant in nearby eastern sites including Ohinetahi Bush Reserve and Hoon Hay Scenic Reserve (Figure 5).

Song Type C is the most western of the observed song types and is composed of eight sites over a distance of 3.35 km (Figure 5). This song type was most numerous at a site in lower Omahu Bush Reserve (-43.665488, 172.611168) but spanned from Ahuriri reserve in the west to Cass Peak in the east (Figure 5).

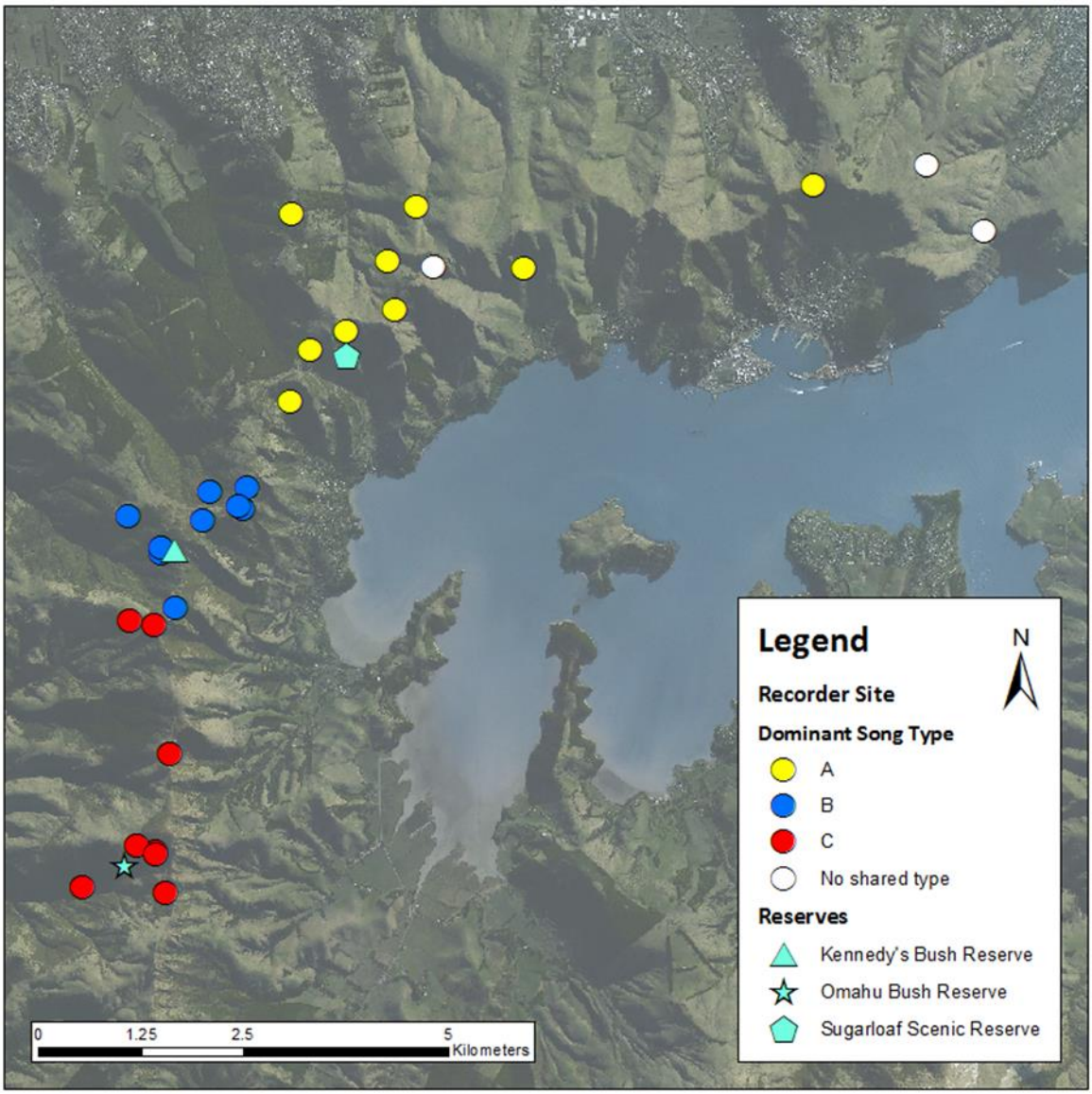

Figure 5: Geographical extent of song type groups. Port Hills source population sites are classified according to dominant song type. The reserves where each song type was most numerous are identified. Basemap image used with permission from CNES 2004-2010/Spot Image.

3.4.2 Urban song types

Source population song types were matched to songs at 22 locations in the greater Christchurch urban area (13 recorder stations, eight incidental recordings) (Figure 6; Figure 7). Most sites were represented by a single song type only, but three of the recorder stations detected a secondary song (Figure 7). Distance to the closest source population site ranged from 1.55 km (Cashmere) to 11.73 km (Lincoln University), actual distances may have been shorter or longer as the precise geographical extent of the dialect groupings are unknown. In 84% (21/25) of cases, the song type detected in an urban location was a match to the dominant song type of the closest potential source population site (Figure 7). A fourth shared song type (Type D) was noted in the urban recordings and shared by eight locations in eastern and northern Christchurch, but did not match any of the song types detected in the Port Hills recordings (Figure 7; Appendix D).

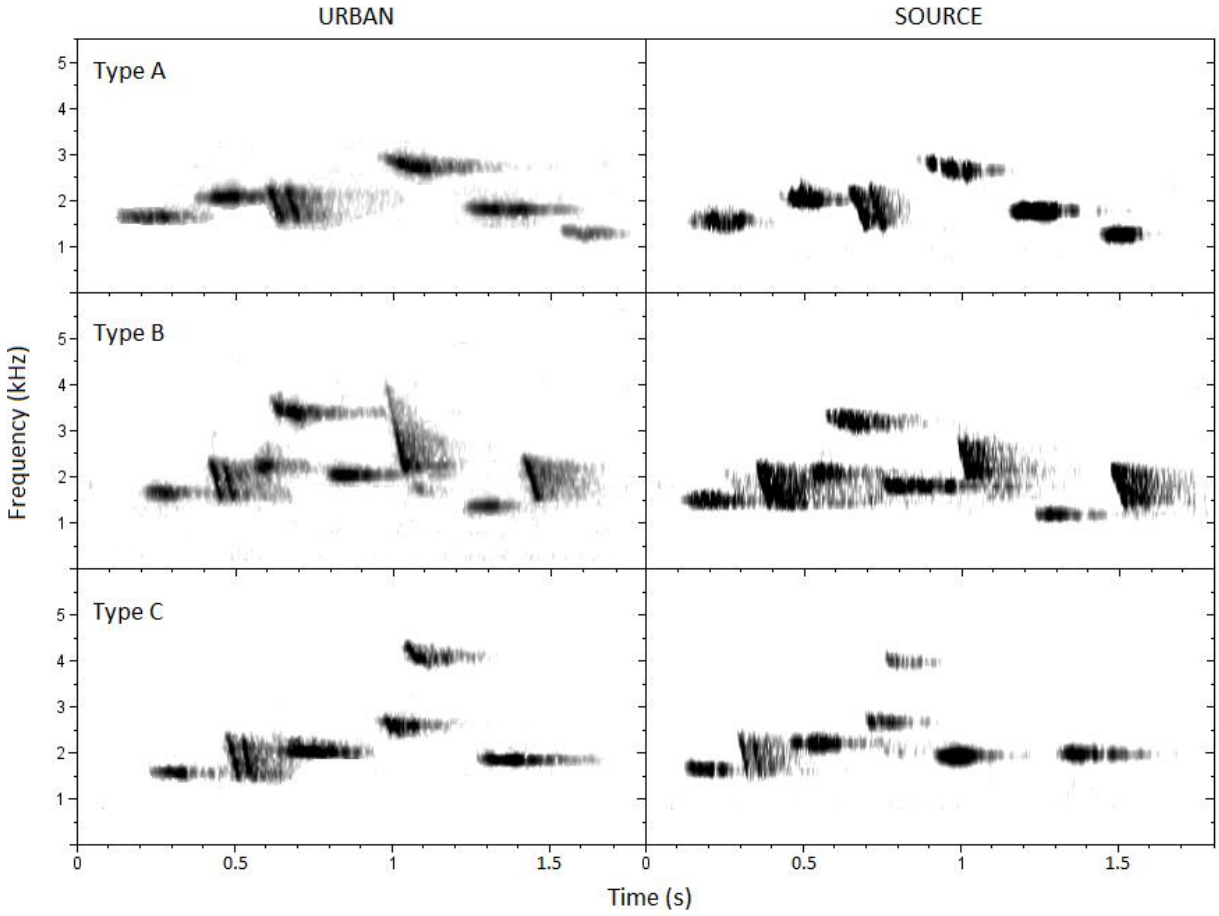

Figure 6: Examples of song type matches between urban and source recording sites. Urban songs depicted are sourced from Cashmere (Type A), Prebbleton (Type B) and Lincoln (Type C)

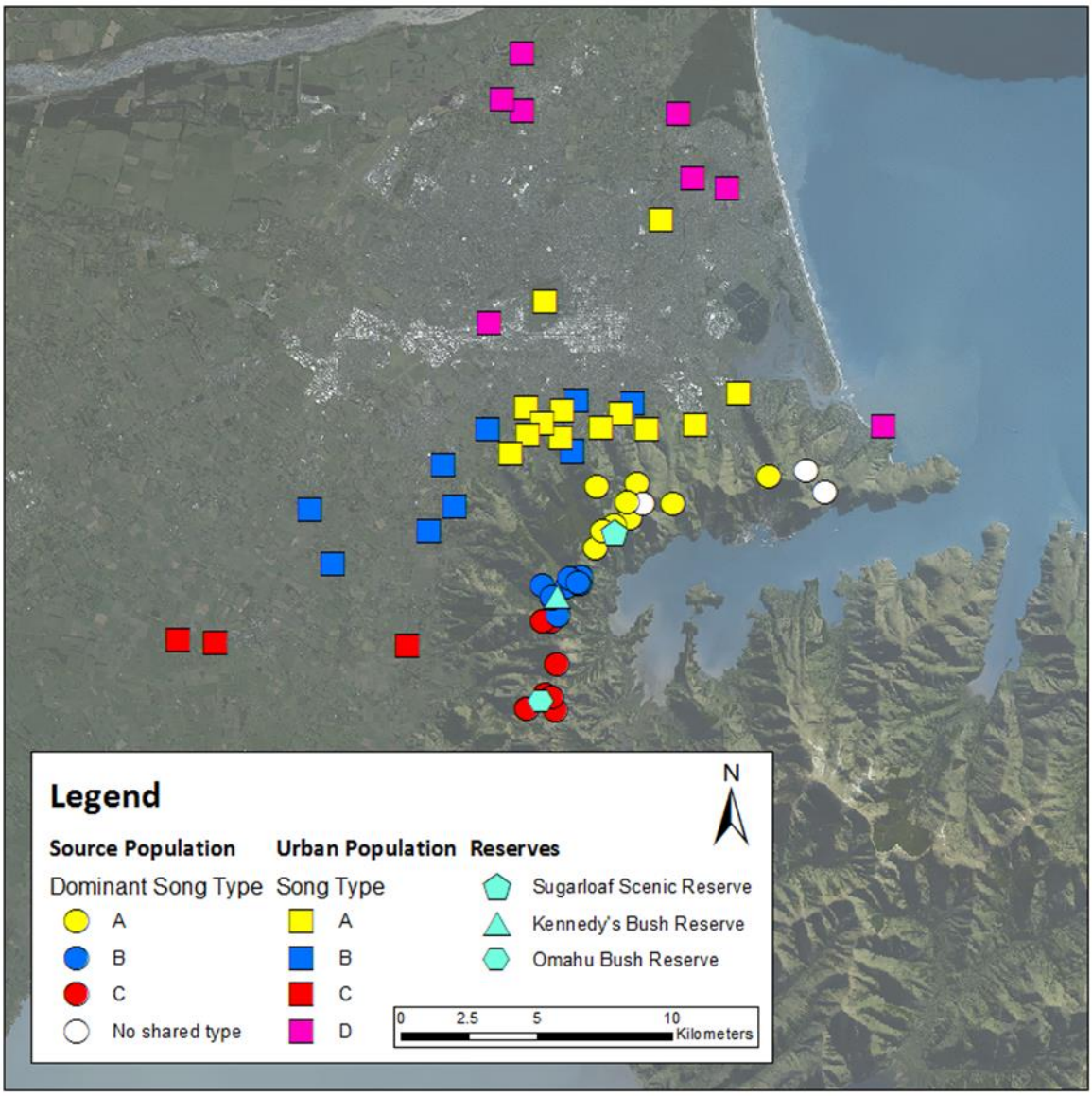

Figure 7: Distribution of source population song types in greater Christchurch area. Basemap image used with permission from CNES 2004-2010/Spot Image

3.5 Discussion

Three main male song type clusters were apparent across the Port Hills bellbird populations. As song types were geographically distinct, they can be considered as fine scale dialectal groups (Podos & Warren 2007). The likely population centres for each dialectal group are Sugarloaf Scenic Reserve (Song Type A), Kennedys Bush Reserve (Song Type B) and Omahu Bush Reserve (Song Type C), which are three of the largest and oldest native bush remnants on the Port Hills. As there are no obvious geographic barriers to dispersal in this case, maintenance of dialectal groupings indicates that individuals may face fitness consequences for non-conformance (Podos & Warren 2007). Such consequences may be social, e.g. harder to hold territories, or reproductive, e.g. female preference for local dialect. Dialects in such a system could be maintained by one of two mechanisms: limited dispersal or vocal imitation (Podos & Warren 2007; Salinas-Melgoza & Wright 2012).

The limited dispersal hypothesis posits that birds remain in their natal areas because they encounter a fitness cost when associating with individuals from other dialectal groups (Baker & Mewaldt 1978; MacDougall-Shackleton & MacDougall-Shackleton 2001). In theory the limited dispersal hypothesis would also result in genetic structuring of dialectal groups (Salinas-Melgoza & Wright 2012). Limited dispersal is unlikely to be solely responsible for dialect maintenance in male bellbirds. Individual bellbirds are, in some cases, known to return to the same sites from year to year (G. Bedford pers. obs. 2017; L. Molles pers. obs. 2007; Brunton et al. 2008b). However, mixing of song types at source population sites indicates that a degree of gene flow is likely occurring between the populations. The vocal imitation hypothesis is perhaps a more likely explanation in this instance.

Vocal imitation posits that immigration does occur to an extent, but dialects are largely maintained because immigrant birds adopt the local dialect (Leader et al 2008; Salinas-Melgoza & Wright 2012). Recent work by Roper et al. (2018) suggests that the initial sensory period in bellbirds, in which birds first memorise a tutor song, lasts approximately three weeks. This initial sensory period would not

allow vocal imitation as it occurs within the period of natal philopatry, however, later acquisition of a non-natal dialect may still be possible beyond this period. True open ended learning by songbirds is rare, but some species have been shown to learn and add new songs to their repertoires beyond this initial sensory period (Trainer & Parsons 2002; O'Loghlen & Rothstein 2002; Wright et al 2008; Alcock 2009; O'Loghlen & Rothstein 2010). It is possible that juvenile male bellbirds may experience a secondary sensory period prior to adult song crystallisation.

A third explanation for dialect maintenance in this context is that the processes of vocal imitation and limited dispersal act cohesively. Salinas-Melgoza & Wright (2012) determined that dialects in yellow naped amazon parrots were maintained by vocal imitation in juveniles and philopatry of adult birds. As dispersal in bellbirds has only been quantified in juveniles (Cresko 2010), or in cases where demographics were uncertain (Brunton et al. 2008a); this combined scenario cannot be ruled out. An assumption of this study is that, even if delayed acquisition occurs, male bellbird vocalisations are stable prior to dispersal.

The presence of all dialectal groups in urban recordings indicates that seasonal dispersal from Port Hills locations into urban environments by male bellbirds is a shared feature of all identified Port Hills populations. Proximity appears to be the biggest factor affecting dispersal as the majority of urban song types were matched to the closest source population dialect. As movements occurred when bellbirds are not breeding, and are largely non-territorial, I assume that assortative mixing within urban environments was not driving these movements. Song Type A (Sugarloaf Scenic Reserve) was detected in Christchurch City, predominantly in the southern suburbs, e.g. Cashmere, Beckenham, St Martins. Song Type B (Kennedys Bush Reserve) largely detected in the south-western outskirts of Christchurch, in Halswell and semi-rural areas adjacent to Tai Tapu and Prebbleton. Song Type C (Omahu Bush Reserve) was detected exclusively west of Christchurch, in Lincoln and Tai Tapu.

Resource tracking is a highly scale dependent process that is influenced by resource distribution patterns and species-specific factors (García & Ortiz-Pulido 2004; Bracis et al. 2015). If large scale resource tracking is a contributing factor to bellbird dispersal behaviour, as has been suggested by Spurr et al. (2010, 2011, 2014), the results of this study suggest that tracking would likely be occurring at a 'patch scale' within the birds' expanded range, rather than at a landscape scale. I have shown that, over winter, bellbirds disperse downhill, occupying an expanded range adjacent to their source populations. This dispersal may be driven by a combination of factors, including reduced territoriality (Craig & Douglas 1986), natal dispersal (Greenwood 1980), low resource availability in source populations (Spurr et al. 2014) and bad weather. Within this expanded range, it is known that birds discover and utilise exotic nectar resources (Spurr et al. 2011, 2014), which may indicate that tracking is occurring in a similar manner to that observed at a local scale within Chapter 2. Patch scale resource tracking, rather than landscape scale tracking, would likely favour dispersal via close resource patches or continuous vegetation patches rather than long distance movements; future research in this area could focus on mapping dialects and dispersal in relation to possible habitat corridors in the greater Christchurch area. It would also be beneficial to examine resource tracking within urban environments, adapting the methodology employed in Chapter 2 to a more sparsely vegetated environment.

The presence of a consistent unknown song type in north and east Christchurch may indicate the presence of an additional source population not identified by my study. The far eastern Port Hills region, around Sumner and Lyttelton, may be a good candidate for such a source population. No shared types were detected in this region, e.g. Jollies Bush and Rapanui Bush, but bellbirds were still present in low densities. Patches of native bush in this area are small and sparsely distributed; a new locally-shared type would have been difficult to detect in these conditions via the automated recording method employed in this study. The alternative source population could also have derived from northern Christchurch; Spurr et al. (2014) noted that there had been reports of bellbirds breeding in Bottle Lake Forest, which is located on the north eastern boundary of the city. This

location was one at which the non-Port Hills shared type was detected. Populations in either location could feasibly be a source for birds in eastern and northern Christchurch city. Systematic manual recording in future studies would allow for a more comprehensive analysis of source population song types than was possible from the data collected in this study. With targeted collection of acoustic data it may also be possible to performed automated classification of song types.

This study suggests that seasonal bellbird dispersal may be more limited than previously thought (Spurr et al. 2011; Spurr et al. 2014). Male bellbird dispersal into Christchurch City each year is probably disproportionately influenced by the closest source populations, e.g. from the Sugarloaf population and the speculated northern/eastern population. Distance limited dispersal may help to explain the findings of Spurr et al. (2014) who reported that although bellbird abundance increased dramatically in Port Hills reserves between 2003 and 2010 as the result of pest control efforts, there was not been a measurable increase in the presence of bellbirds in domestic gardens within the city during the same time. A large proportion of the observed population growth in the Port Hills reserves was attributed to Kennedys Bush (Spurr et al. 2014), which according to the results of this study (Song Type B), would have led to greater spill over into surrounding areas such as Halswell, but would not have driven a city wide increase. In accordance with the idea that increased abundance on the Port Hills would lead to an increased presence of bellbirds in adjacent areas only, a gradual increase in bellbird abundance in south western Christchurch suburbs (Hoon Hay, Wigram, Cashmere, and Somerfield) has been recorded over the past decade (Jon Sullivan, unpublished data).

Distance limited dispersal by Christchurch bellbirds also has implications for the wider understanding of male bellbird dispersal behaviour. It has previously been established that bellbirds are capable of dispersing over large distances (Craig & Douglas 1986; Brunton et al. 2008a); however, on the basis of these findings, it appears likely that the majority of bellbird movements occur on a more restricted scale. Limited dispersal from source populations is supported by the findings of Cresko

(2010) who tracked dispersal of juvenile bellbirds from the Zealandia nature reserve in Wellington. They reported a maximum travel distance of 0.66 – 3.45 km (average 1.84 km). These short travel distances are more equivalent to the dispersal observed in this study than in Brunton et al. (2008a). Limited movement by non-breeding bellbirds may also modify our understanding of the functional role of bellbirds within native ecosystems. Bellbirds are key pollinators, and dispersal agents for many native species. Despite the widespread population of bellbirds throughout the South Island, many flowering plant species are becoming pollination- and dispersal-limited (Montgomery et al. 2001; Murphy & Kelly 2001; Robertson et al. 2008). Distance limited dispersal may be an important contributing factor to this. Montgomery et al. (2001) examined pollination limitation in *Fuchsia perscandens* at two sites on Banks Peninsula: Buckleys Bay and the Tors. Although plants at both sites were pollination limited, fruit set was significantly higher at Buckleys Bay where there was a resident bellbird population, compared with the Tors site, which was just 3.4 km east. Based on the results of this study, it could be speculated that bellbird distance limited dispersal could explain the lower fruit set at the Tors site.

3.6 Conclusion

Bellbird populations on the Christchurch Port Hills form three dialectal groups. All three male song dialects were detected in urban environments following a seasonal dispersal movement. In the majority of cases, urban song types were matched to the closest source population. This proximity-governed dispersal indicates that if large scale resource tracking is occurring, it is likely occurring within the birds' seasonally expanded ranges rather than at an across landscape level, and further suggests that bellbird movements may be more distance limited than previously assumed.

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Chapter 4

Memory informed foraging by bellbirds (*Anthornis melanura*) and the importance of resource value

4.1 Abstract

Many nectarivores rely on memory informed foraging to increase the efficiency of resource exploitation. In New Zealand, nectarivores experience large variation in nectar quality due to the predominance of unspecialised pollination systems. I assessed spatial memory in bellbirds (*Anthornis melanura*) in order to determine the role that variable reward value plays in the formation and retention of memories. Free-living, adult male bellbirds were presented with experimental arrays consisting of four free-standing sugar water feeders. In each trial one sugar water feeder was supplied with a relatively high concentration of sugar water (7%, 10%, 15% or 20% sucrose) while the remaining three feeders contained a low-concentration sugar water solution (5% sucrose). Initial visitation to the array was not different from random. Following a single encounter with the higher-concentration feeder, individuals preferentially returned to the most rewarding feeder in 85-95% of foraging bouts. Little variation in accuracy was observed between concentration treatments within the 48 hour trial period. At a longer retention interval of 20 days, high value reward information was retained with greater accuracy. These findings demonstrate that bellbirds are motivated to use spatial memory to return to resources when the variation in concentration is as little as 2%. Given sufficient motivation to exploit a resource, both small and large differences in nectar quality equally affect memory informed foraging over short term timescales. Slower decay of high value information likely affects foraging choices over longer timescales.

4.2 Introduction

Nectar is a highly variable resource. The composition and temporal availability of nectar vary markedly among different plant taxa (Rathcke 1992). Variability is exacerbated by abiotic factors (e.g. humidity and rainfall) and biotic factors (e.g. competition and genetic variation) which cause inconsistent nectar rewards at between-individual and within-plant levels (Rathcke 1992). Reliance on a patchily distributed, stationary resource of such highly variable quality has led to widespread adoption of memory informed foraging strategies across a range of nectivorous species (Garber 1988; Cartar 2004; Henry & Stoner 2011; Pérez et al. 2011).

Memory informed foraging is a two stage process involving the acquisition and retention of relevant information. Initially, foragers acquire information about resources within their foraging environment through experience, e.g. location, quality, and current availability (Stephens 2007). Resource information is then encoded and stored as memories which can be retrieved in a relevant context in order to inform decision making and subsequent behaviour (Stephens 2007). Memory informed foraging can increase an individual's fitness by reducing energy expenditure during resource acquisition (Bracis et al. 2015). Foragers are able to return to highly rewarding resource patches without investing additional time and energy in searching (Stephens 2007; Fagan et al. 2013; Bracis et al. 2015). Less time spent foraging can reduce the risk of predation (Kie 1999) and allows greater investment in other behaviours, such as territorial defence (Araya-Salas et al. 2018).

Investment in informed foraging behaviours, while beneficial in many contexts, incurs a cost. Gathering, storing and updating information requires diversion of time, energy and attentional capacity away from other behavioural processes, and can increase exposure to adverse conditions (Clark & Dukas 2003; Dall et al. 2005; Hall et al. 2007; Stephens 2007). Memory informed foraging is a beneficial strategy only when the acquired knowledge leads to a behavioural change which has a net positive consequence for individual fitness (Dall et al. 2005). If foragers are unable to modify

their behaviour, or behavioural shifts are possible, but do not provide a fitness gain, then there is little motivation to gather and retain foraging information (Dall et al. 2005; Stephens 2007). The potential value of information, and expected investment in informed foraging behaviours, can be influenced by many factors such as forager constraints, e.g. dietary specialisation (Henry & Stoner 2011), and resource characteristics such as variability or distribution (Bracis et al. 2015).

There are three main lineages of nectar feeding birds worldwide, the hummingbirds (Trochilidae) of North and South America, the sunbirds (Nectariniidae) of Africa and Asia, and the honeyeaters (Meliphagidae) of Australasia (Nicholson and Fleming 2003). Adaptation for nectar feeding evolved independently in each of these groups and has resulted in differing levels of specialisation (Nicholson & Fleming 2003; Fleming & Muchhala 2007). Hummingbirds are the most phenotypically specialised taxa (Pyke 1980, Fleming & Muchhala 2007; Nicholson & Fleming 2014). A consequence of specialisation for nectar feeding in hummingbirds is that they have exceptionally high mass-specific metabolic demands (Beuchat et al. 1990). The high cost associated with visiting a low value or depleted resource has selected for advanced cognitive abilities and memory informed foraging in many cases. A combination of laboratory and field studies have demonstrated that hummingbirds can remember the location, content and schedule of nectar production for individual flowers, and use this information to increase their foraging efficiency (Henderson et al. 2001; González-Gómez & Vásquez 2006; González-Gómez et al. 2011; Pérez et al. 2011; Jelbert et al. 2014).

Memory informed foraging has also been documented within the honeyeater family, although it has not been examined as widely as with hummingbirds (Burke & Fulham 2003 *Anthochaera Phrygia*; Sulikowski & Burke 2010 *Manorina melanocephala*). Honeyeaters are less phenotypically specialised for nectar feeding than hummingbirds (Nicholson & Fleming 2014) and often consume more varied diets (Pyke 1980). Floral interactions involving honeyeaters are also less specialised than those involving hummingbirds (Fleming & Muchhala 2007; Zenata et al. 2017). Lower dietary and interaction specialisation may have led to differences in the nature and extent of informed foraging

behaviours, but this has not been quantified in the context of avian nectarivores (Henry & Stoner 2011). Less specialised individuals are more readily able to switch to alternative resources and this may limit the benefit to be gained from recursive visitation in some contexts. Greater diet variability and flexibility may also increase the potential influence of resource characteristics on the value of information. No prior attempt has been made to quantify how variation in reward characteristics affects memory in nectivorous birds.

New Zealand is a good system in which to examine the role of resource value in informed foraging, because resident avian nectarivores consume an extremely varied nectar diet. Pollination mutualisms in New Zealand are usually unspecialised and imprecise (Newstrom & Robertson 2005). The vast majority of avian floral visits (89%) are carried out by just three species: two endemic honeyeater species, the tūī (*Prosthemadera novaeseelandiae*) and the bellbird (*Anthornis melanura*), and the self-introduced, opportunistic nectarivore, the silvereye (*Zosterops lateralis*) (Kelly et al. 2006). Both honeyeater species have a preference for nectar feeding, but will switch to a largely insectivorous or frugivorous diet when nectar is not available (Craig et al. 1981). The bellbird, in particular, has a highly insectivorous diet in some regions (Murphy & Kelly 2003). Just 1% of indigenous floral species are morphologically typical of the ornithophilous syndrome (Lloyd 1985). Due to the low diversity of ornithophilous species, entomophilous flowers form a significant part of honeyeater nectar diets (Castro & Robertson 1997; Spurr et al. 2011). As a result of their varied diet New Zealand honeyeaters experience substantial variation in nectar concentration (7 – 47%), volume, and floral structure (Bergquist 1987; Rasch & Craig 1988).

The aim of this study was to examine memory informed foraging within this less specialised nectarivore system. Bellbirds, the most common honeyeater species on the South Island of New Zealand, were exposed to open field maze trials derived from similar studies of hummingbirds (Hurly 1996; Gonzalez-Gomez 2006; Araya-Salas et al. 2018). Bellbirds are less physiologically specialised than hummingbirds, but likely to have faced similar selection pressures associated with nectar

foraging. Therefore, I expected that individuals would be capable of learning the position of a highly rewarding feeder within an experimental array. I further expected that, because bellbirds are facultative nectarivores and experience broad variation in nectar quality and concentration, individuals would demonstrate value-dependent investment in informed foraging. Information concerning the location of high value rewards is expected to be retained more accurately, and over longer time intervals.

Hypotheses:

1. I expected that bellbird initial feeder choice within a novel array would be random, indicating that they were not using cryptic cues, such as scent, to locate the feeder with the highest reward. I additionally expected that an individual's initial accuracy would not improve over multiple trials; further demonstrating that they were not learning to use olfactory cues to locate high-reward feeders.

2. I expected that once an individual had located the highest-reward feeder in an array, that they would preferentially return to that feeder, indicating that they remembered its location.

3. I expected that the accuracy of return visits would increase with the quality of the reward (i.e. higher sugar concentration), indicating that higher-value information was retained with greater accuracy than lower-value information.

4. I expected that, after a withholding period, bellbirds would return to the most rewarding feeder with greater accuracy when reward quality (sugar concentration) was higher.

4.3 Methodology

4.3.1 Subjects and location

Trials using artificial feeders were conducted at two locations in Canterbury, New Zealand, between July - September 2016 and April - December 2017 (Takamatua 42.79'S, 172.96'E, Christchurch City 42.58'S, 172.63'E). Both locations were large urban gardens in close proximity to patches of native vegetation where bellbirds forage for nectar. Subjects were banded, free-living adult male bellbirds that had prior experience using a variety of artificial feeders. Females were infrequent visitors to artificial feeders and were not included in this study (Appendix E). Bellbirds did not defend the feeders throughout most of the year, which allowed visitation by multiple individuals in rapid succession or even simultaneously. Aggression during the breeding season (September - January) occurred, but at a low level; when aggression did occur, temporarily excluded birds were able to feed as soon as the aggressor finished using the feeder.

4.3.2 Feeder training

Bellbirds were trained to use free standing artificial feeders during June 2016 and March 2017. The feeders were 1.6 m in height and contained a 1 litre reservoir of sugar water to ensure the resource was not depleted (Figure 8: Un-banded bellbird using an experimental feeder during the training phase of experimental trials (March 2017). During training, two feeders were positioned 1 m apart. One contained a low concentration of sugar water (5% sucrose) and the other contained a high concentration of sugar water (20% sucrose). Training feeders were positioned >2 m from all future experimental sites. Pilot trials in Christchurch indicated that at a distance of 2 m there was no bias towards any particular experimental feeder in a newly established array.

Figure 8: Un-banded bellbird using an experimental feeder during the training phase of experimental trials (March 2017)

4.3.3 Study precedent

Previous research examining memory informed foraging in medium sized nectarivores (e.g. honeyeaters and sunbirds) has been conducted under controlled conditions using captive individuals (Sulikowski & Burke 2007; Sulikowski & Burke 2010; Whitfield et al. 2014). No precedent exists for studying the cognitive abilities of free-living honeyeaters in the wild, however, recent studies in the field of avian cognition have emphasised the importance of doing so (Pritchard et al. 2016; Cauchoix et al. 2017; McCune et al. 2019). The basis for experimental work in this chapter was influenced by the González-Gómez &Vásquez (2006) spatial memory trial in free living Green-Backed Firecrown Hummingbirds (*Sephanoides sephaniodes*). The basic experimental design used in this study was adapted to bellbirds, and to my specific research objectives, over an extensive pilot study period

spanning April – June 2016 which included work at the Christchurch experimental site and with a population of birds in Kennedys Bush forest reserve, Christchurch, New Zealand.

4.3.4 Trial procedure

Four identical feeders were set up in 1 m x 1 m square array with at least 1 m clearance from surrounding vegetation (Figure 9). At the start of each trial one randomly chosen feeder was filled with 1 litre of high concentration sugar water [High concentration feeder, HCF], while the other three feeders were filled with 1 litre of low concentration sugar water (5% sucrose) [Low concentration feeder, LCF] (Figure 9). In cases where sugar water was exhausted before the end of the trial, it was replenished.

Individual visitation was assessed in two phases: the search phase and the return phase. The search phase was defined as the period from the bird's first visit to the array until the point when the HCF was sampled. All subsequent visits to the array were defined as the return phase. Successive visits that occurred within a five minute period of an arrival at the array were considered part of the same visitation bout. Two cameras (Ltl Acorn 5310A model), positioned at opposite ends of the array, recorded time-lapse images (capture rate: two images every two seconds) during sunlight hours to assess visitation. A pilot study determined that this was the most accurate camera set up, and that feeding visits were reliably captured using this approach. Comparison with 1 hr periods of live visual observation were used to ensure the accuracy of this approach during pilot studies and throughout experimental trials. Visual observation sessions assessed whether all feeding visits were captured in time lapse imagery, and whether visits were correctly classified as feeding/non-feeding based on the image. Trials were not run during periods of rainfall to avoid dilution of sugar water.

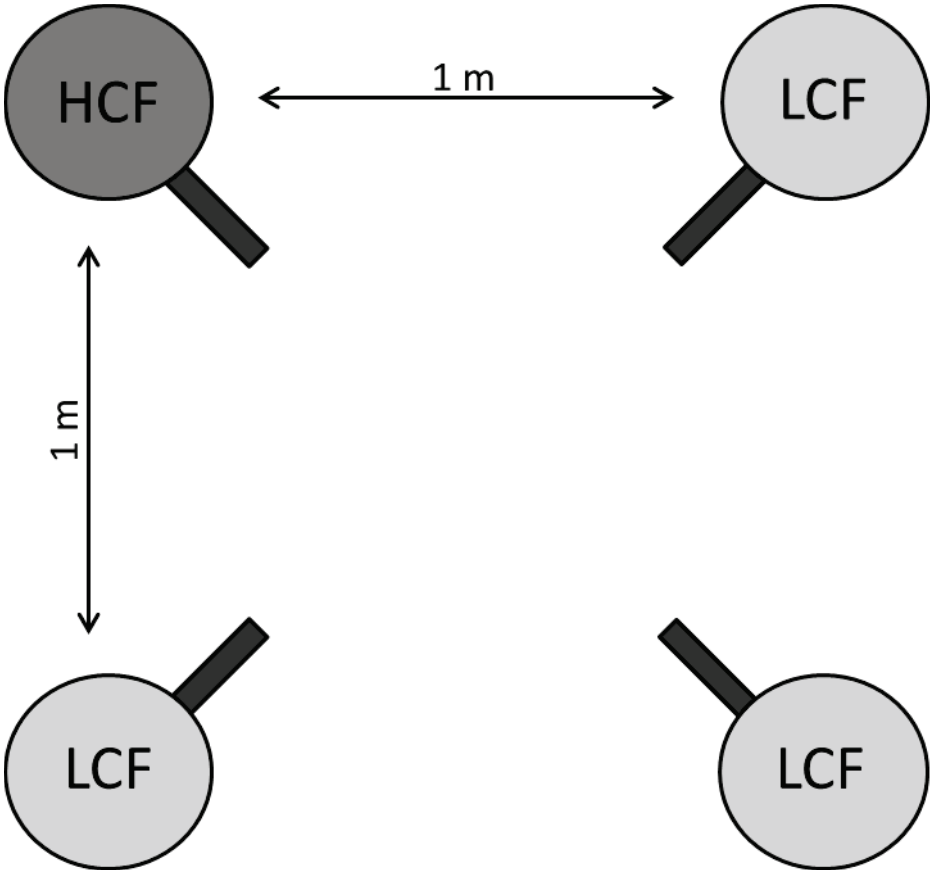

Figure 9: Experimental array configuration. The position high concentration feeder (HCF) was randomly determined in each instance and varied in concentration between treatments. The three low concentration feeders (LCF) contained 5% sucrose solution in all trials. Perches faced into the centre of the array to retain symmetry and ensure the array appeared consistent regardless of approach direction.

Experiment 1: Accuracy

HCF concentration was presented at four different treatment levels (7%, 10%, 15% and 20% sucrose). This range was chosen to reflect the typical concentration of bird-pollinated plant nectar worldwide (8-12% for opportunistic nectarivores and 15-25% for specialist nectarivores; Johnston and Nicholson 2008), and the lowest concentration of nectar known to be consumed by New Zealand honeyeaters (7%; Bergquist 1987). During trials, participants were allowed to visit the array freely over a period of 48 hours. Each concentration treatment was run at four experimental sites within the study locations (three sites in Takamatua, one in Christchurch). The order of treatments

was randomly determined for each site. Visitation varied between trials in response to the flowering of natural food sources nearby (within 200 m). Once trials had been conducted across all concentration treatments, additional trials were conducted until a minimum of 20 banded birds had participated at each concentration.

Once the search phase had been completed, i.e. the individual had visited the HCF feeder, individual performance was assessed as the proportion of all return bouts in which the first visit to the experimental array was to the HCF (bout success). A minimum of five return bouts was used as a threshold for individual inclusion in further analysis. The proportion of the first five bouts that were successful (first visit to HCF) was included as an additional performance variable to account for variation in individual visitation (initial success; this was equivalent to bout success for birds that only made five return visits). Visits to LCFs that occurred following an initial encounter with HCF were considered to be sampling visits; the proportion of bouts in which sampling occurred was also calculated (sampling rate).

Following each trial there was a reset phase of one week in which the array was replaced by a single HCF (corresponding to the concentration to be used in the next trial treatment). A pilot study indicated that this reset phase was sufficient to remove bias in the search phase of the next trial.

Experiment 2: Retention

The duration of memory retention was assessed across two HCF concentration treatments; 10% and 20% sucrose. For these trials an array, identical to that described in Experiment 1, was established at the Takamatua site and maintained for a period of five days ("0 day" withholding period). During this initial training period resident birds were able to visit and learn the location of the HCF. The array was removed without a reset phase for a period of 20 days. After 20 days, the feeders were reinstated in their original positions and individual visitation was recorded ("20 day" withholding period). The array was left up for five days to allow birds to relearn or reinforce the location of the

HCF (secondary training period). Feeders were then removed again for a longer 40 day period. After 40 days, feeders were again reinstated and visitation was recorded over a shorter 48 hour period as no further training was required ("40 day" withholding period").

Individual performance during the retention trials was determined by the number of feeder visits that were required to initially locate the HCF (number of search visits). This was calculated during the initial training period (0 day) and then separately after the 20 day and 40 day withholding periods. All exploratory visits to were included irrespective of whether or not they occurred within the same foraging bout. Participation in retention trials was dependent on prior exposure as individuals were required to participate (>5 visits to HCF) in all preceding trial stages, i.e. birds were only considered at the 40 day withholding period if they were present during initial training and visited the array after the 20 day withholding period. Three trials at each concentration were conducted at different experimental sites within the Takamatua location.

4.3.5 Statistical analysis

All statistical analysis was carried out using SPSS version 20 (IBM Corp. 2011).

Experiment 1: Accuracy

Search phase accuracy and potential use of olfactory cues

Search phase visitation (number of visits before locating HCF) at each concentration treatment was compared to the median number of visits expected in a random foraging scenario (2.4, based on the geometric random distribution) using a one-sample t-test. The geometric random distribution is a discrete probability distribution which represents the number of independent Bernoulli trials required to get one success assuming a constant probability of success ($p = 0.25$). In cases were individuals participated in multiple trials within a single concentration treatment, average visitation was used in the analysis. If birds were relying on olfactory information to locate the highest-

concentration feeder, search phase visitation would be expected to be biased towards the HCF rather than random.

Nectar foraging birds typically have a poor sense of smell and rely primarily on sight during the location of floral resources (Cronk & Ojeda 2008). A repeated measures ANOVA was performed to eliminate the possibility that olfaction was influencing trial results. The dependant variable was the total number of feeders encountered during the search phase (i.e. range of 1 – 4) and was assessed across all four concentration treatment levels. The analysis only included the 21 individuals who had completed trials across all concentration treatments. In cases where individuals had participated in multiple trials at a particular treatment, the first instance was used. If birds were relying on olfactory cues, fewer mistakes are expected when locating the HCF in higher concentration trails as the signal will be strongest in these instances.

Another repeated measures ANOVA was performed to determine whether search behaviour became more efficient with experience. Fourteen individuals who had completed three 20% treatment trials in 2017 were included in the analysis. The dependent variable was the total number of feeders encountered during the search phase (i.e. range of 1 – 4) and was compared across the three levels of experience (first trial, second trial. third trial). Only 20% trials were examined as olfactory cues should have been strongest in this instance.

Return phase visitation

Initially, Cochran's Q tests were performed to justify the use of combined measures as indicators of return phase performance. Cochran's Q tests assess that the marginal probability of success (visitation to HCF) is unchanged across related treatments (1^{st}, 2^{nd}, 3^{rd}, 4^{th}, 5^{th} visit). A non-significant result indicates that return phase visits can be combined. Separate analyses were performed for each concentration treatment.

As for search phase visitation, return phase visitation (bout success) at each concentration treatment was and compared to the proportion of visits expected by chance (0.25) using a one sample t-test. In cases were individuals participated in multiple trials within a single concentration treatment, average visitation was used in the analysis.

I used linear mixed effect models to determine the effect of concentration treatment on individual performance measures. Performance variables (bout success, initial success, sampling rate) were arcsine square root transformed prior to analysis. The transformed performance variables were modelled as the dependent variables in separate analyses. Concentration treatment was included as a fixed effect. To account for non-independence of samples, individual identity was included as a subject variable with correlated random effects. Experimental site was included as a random effect. Model covariance structure was chosen based on resulting AIC values. Significant effects were further analysed using Sidak's t-test to account for multiple comparison. To facilitate interpretation, untransformed means ± standard errors are reported.

Potential use of conspecific cueing

As bellbirds did not exclude conspecifics from the experimental array it is important to consider the possibility that bellbirds used social cues to aid in the location nectar rewards. I modelled a generalised estimating equation with binomial error structure and logit link function to determine if individuals performed more or less accurately in the presence of other birds. Predictor variables were the presence of a conspecific at the HCF at the time of array visitation (within 30 seconds of approach) and concentration treatment. The binary response term was the success or failure of the initial search phase. The first visit was used, as social information should have been most valuable in this instance. Bird ID was included was a subject variable with correlated random effects.

A linear mixed effect model was also created to examine the role of conspecifics on overall trial behaviour. Trial averages were calculated for search phase visitation, bout success, and sampling

rate. Search phase visitation was square root transformed; bout success and sampling rate were arcsine square root transformed. These variables were modelled as dependent variables in separate analyses. Concentration treatment, presence of aggression, and number of conspecifics were included as fixed effects in the models. Aggression was a binary response relating to the presence or absence of exclusionary behaviour by a dominant bird. Aggression by a dominant bird was assessed by direct observation and through photo analysis and was characterised by the monopolisation of resources which occurred in the absence of feeding behaviours. The number of conspecifics present in each trial was estimated based on the number of banded individuals that visited the array throughout the trial process and was divided into six categories: 1-5, 6-10, 11-15, 16-20, 20-25, 25-30 individuals. Experimental site was included as a random effect. Model covariance structure was chosen based on resulting AIC values.

Experiment 2: Retention

Memory retention was also examined using linear mixed effect models. The dependent variable, number of search visits required to locate the HCF, was square root transformed prior to analysis. Subject identity as a function of site was included as a subject variable with correlated random effects. Concentration treatment, withholding period (0 day, 20 day and 40 day) and an interaction term were included as fixed effects. Withholding period was specified as a repeated measure. Training (number of visits in the preceding training stage) and site were included as random effects. Separate models were created for the low (10%) and high (20%) concentration treatments. Model covariance structure was chosen based on resulting AIC values. Significant effects were further analysed using Sidak's t-test to account for multiple comparison. I report untransformed means ± standard errors for easier interpretation.

Search phase visitation at each withholding period was compared to the median number of visits expected in a random foraging scenario (2.4, based on the geometric random distribution) in a series of one sample t-tests, as per Experiment 1. 20% and 10% treatment data were analysed separately.

4.4 Results

4.4.1 Experiment 1: Accuracy

Search phase accuracy and potential use of olfactory cues

A total of 43 banded individuals participated in at least one trial. In the search phase, individuals made a mean of 2.55 ± 0.12 visits to the array before encountering the HCF. The search phase encounter rate was not significantly different than that expected from random visitation in any of the concentration treatments ($0.071 \geq p \leq 0.59$; Figure 10). Concentration treatment, and therefore the potential gradient of any olfactory signal, did not affect the number of feeders visited during the search phase visits by individual birds ($F_3 = 1.27$, $p = 0.293$). Individuals also did not become more efficient at locating the HCF during the search phase with experience ($F_2 = 0.576$, $p = 0.569$).

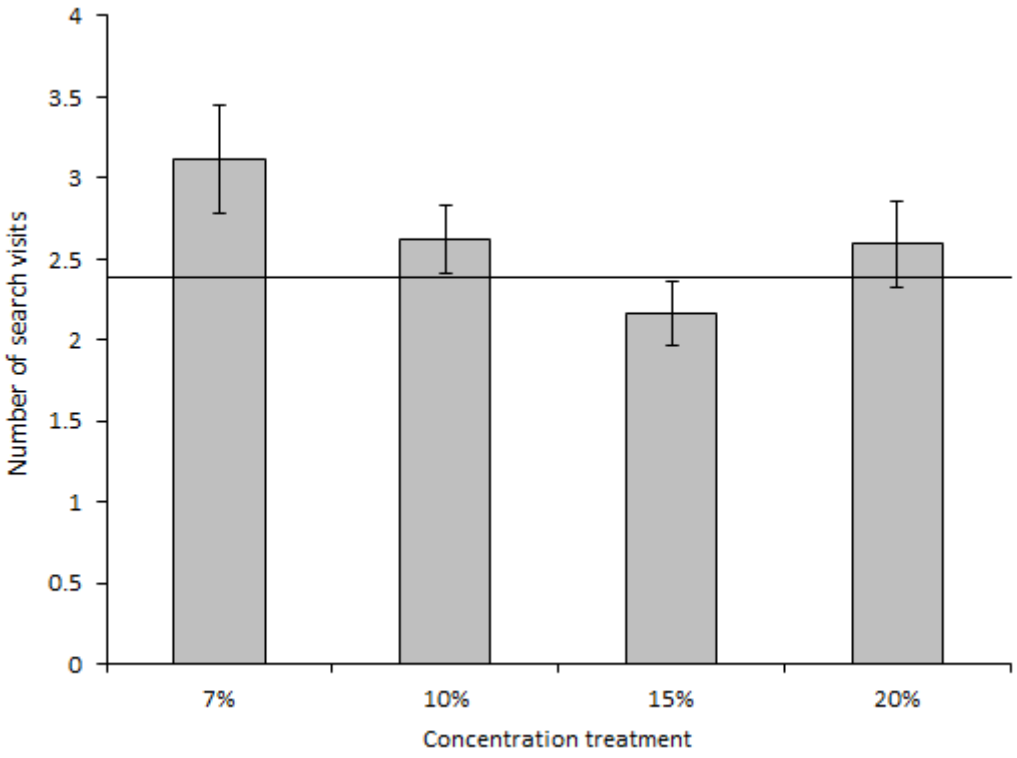

Figure 10: Mean number of search phase visits performed in accuracy trials. Horizontal line indicates number expected in a random foraging scenario (2.4). Error bars indicate standard error of mean.

Return phase visitation

Return phase accuracy did not improve with successive visitation in any concentration treatment, justifying the use of combined performance measures (7% Cochran's $Q_4 = 7.12$, $p = 0.133$; 10% Cochran's $Q_4 = 8.97$, $p = 0.062$; 15% Cochran's $Q_4 = 8.14$, $p = 0.086$; 20% Cochran's $Q_4 = 5.92$, $p = 0.205$). Return phase performance (Proportion of total visits to HCF) was significantly better than expected by chance across all of the concentration treatments (7% $t_{22} = 15.5$, $p < 0.001$; 10% $t_{33} = 60.8$, $p < 0.001$; 15% $t_{28} = 40.46$, $p < 0.001$; 20% $t_{28} = 50.49$, $p < 0.001$; Figure 11).

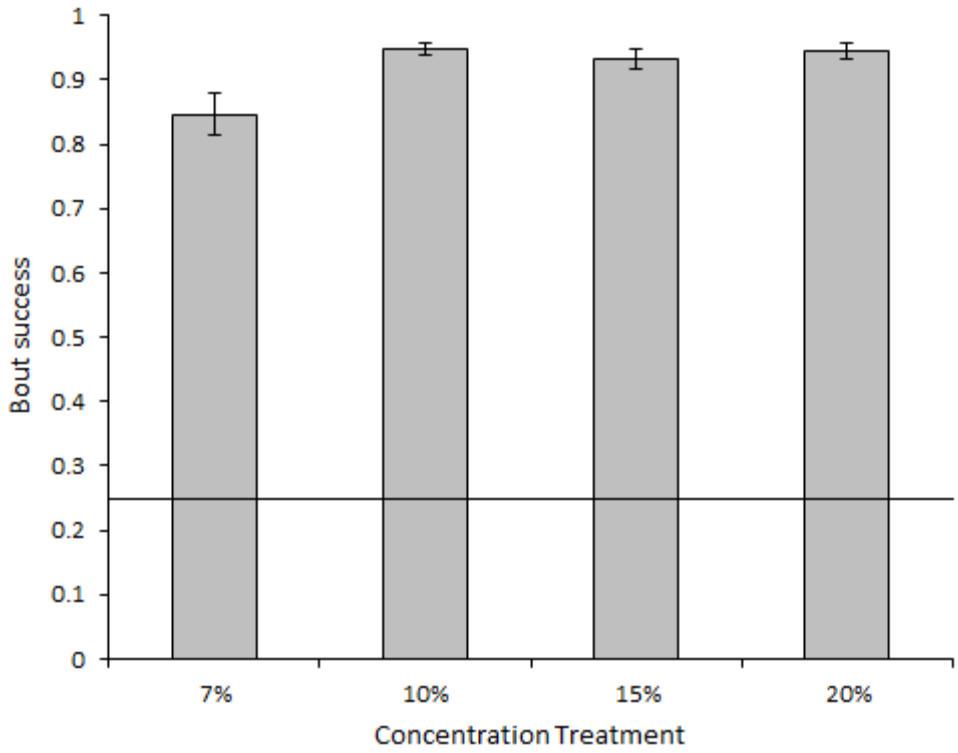

Figure 11: Mean bout success during return phase in accuracy trials. Horizontal line indicates the proportion expected in a random foraging scenario (0.25). Error bars indicate standard error of mean.

There was a significant effect of concentration treatment in models of both trial performance measures (Bout success: $F_{3,173} = 6.765$, $p < 0.001$, Initial success: $F_{3,168} = 8.79$, $p < 0.001$). In both trials, performance in the 7% treatment (Bout: 0.84 ± 0.02, Initial: 0.85 ± 0.02) was significantly lower than performance in the 10% (Bout: 0.95 ± 0.01, Initial: 0.94 ± 0.01), 15% (Bout: 0.94 ± 0.02, Initial: 0.93 ± 0.02), and 20% (Bout: 0.95 ± 0.01, Initial: 0.96 ± 0.01) treatments (Table 2; Figure 11). No significant difference was noted between the three higher concentration treatments (Table 2; Figure 11). There was also a significant effect of concentration treatment on sampling rate ($F_{3,185} = 31.8$, $p < 0.001$). The 7% (Sampling: 0.17 ± 0.01) treatment had a significantly higher occurrence of sampling behaviour than all other treatments (Table 2; Figure 12). The 10% treatment (Sampling: 0.05 ± 0.01) also had a higher rate of sampling than in the 15% (Sampling: 0.02 ± 0.01) and 20% trials (Sampling:

0.03 ± 0.01) (Table 2; Figure 12). No difference was observed between the 15% and 20% trials (Trial 1; Figure 12).

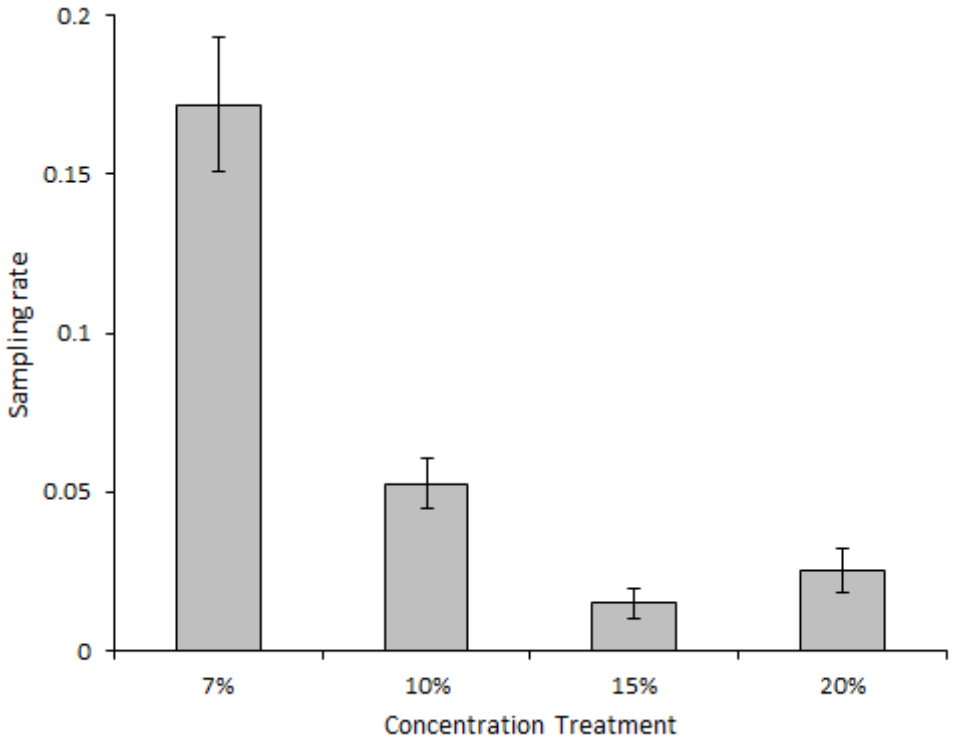

Figure 12: Mean sampling rate during return phase in accuracy trials. Error bars indicate standard error of mean.

Table 3: Pairwise comparisons tests performed on trial accuracy data. Values provided are Sidak adjusted p-values. Significant values at α = 0.05 level are indicated by *.

Treatment levels (%)	Bout Success	Initial Success	Sampling Rate
7 vs. 10	**0.001***	**0.001***	**<0.001***
7 vs. 15	**0.008***	**0.010***	**<0.001***
7 vs. 20	**<0.001***	**<0.001***	**<0.001***
10 vs. 15	0.998	1.000	**0.012***
10 vs. 20	1.000	0.464	**0.026***
15 vs. 20	0.983	0.399	0.995

Potential use of conspecific cueing

The majority of initial array visits did not occur in the presence of a conspecific (66.8%). Subsequent visits were also largely performed in the absence of conspecific cues (75.8% of first five array visits). Initial search phase success was not significantly affected by the presence of a conspecific (Wald X^2_1 = 0.001, p = 0.981) nor by concentration treatment (Wald X^2_3 =0.241, p = 0.971). There was also no significant effect of aggression or number of participants on mean trial search phase visitation, return bout accuracy or sampling behaviour ($0.35 \leq p \leq 0.80$).

4.4.2 Experiment 2: Retention

A total of 36 individuals participated in at least one retention trial (25 in 10% trials, 34 in 20% trials). Participation was lower in the 40 day retention interval testing due to the constraints of prior exposure (14 in 10% trials, 21 in 20% trials).

Concentration treatment and withholding period had significant effects on performance in retention trials (concentration: $F_{1, 75}$ = 4.14, p= 0.045; withholding period: $F_{2, 82}$ = 19.4, p<0.001). The interaction

term was also significant ($F_{2, 82} = 0.25$, $p<0.001$). In the 10% trials there was no significant difference between the 0 day (Search: 2.10 ± 0.15), 20 day (Search: 2.10 ± 0.16), and 40 day (Search: 2.22 ± 0.20) withholding periods ($F_{2, 119} = 0.264$, $p=0.768$; Figure 13). There was a significant difference between withholding periods in the 20% trials ($F_{2, 108} = 38.38$, $p < 0.001$). After a withholding period of 20 days, significantly fewer search phase visits were required to locate the HCF (Search: 1.19 ± 0.07) than in the 0 day (Search: 2.16 ± 0.14, adjusted $p < 0.001$) or the 40 day (Search: 2.21 ± 0.15, adjusted $p < 0.001$) withholding period (Figure 13). The 40 day withholding period visitation was not significantly different from the 0 day period (adjusted $p = 0.969$) (Figure 13).

One sample t-tests confirmed that non-random visitation only occurred in the 20%, 20-day trials ($t_{34} = -11.99$, $p<0.001$). Search phase visitation across all other withholding periods did not significantly differ from that expected by random visitation ($0.116 \geq p \leq 0.357$).

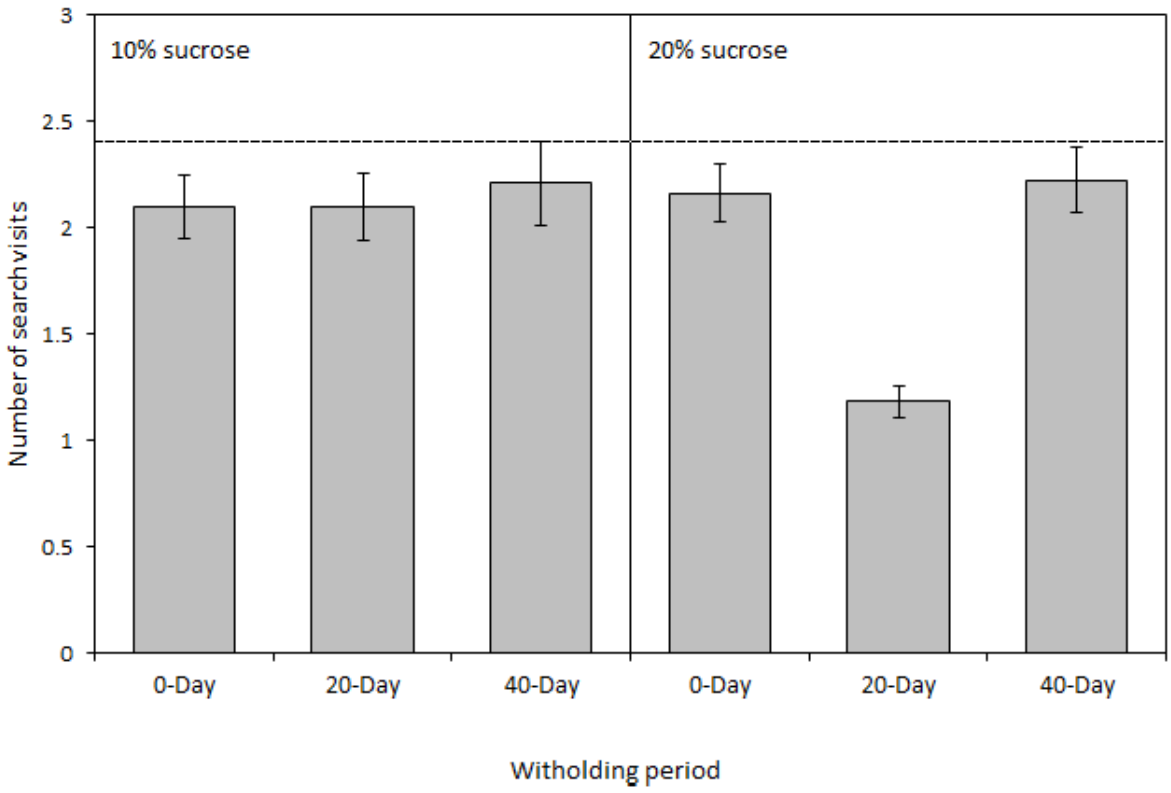

Figure 13: Mean search phase visitation following a 0, 20, and 40 day withholding period in 10% and 20% sucrose retention trials. Error bars indicate significant error of mean. Dashed line indicates number of search visits expected by random visitation (2.4)

4.5 Discussion

Bellbirds have the cognitive capabilities required to adopt a memory informed foraging strategy in response to variation in nectar quality. Initial exposure to experimental arrays was characterised by random visitation, which indicates that external goal-specific cues, such as sight and smell, did not signal the position of the HCF to foraging birds. Olfactory cues were further eliminated as a potentially confounding factor as initial visitation to novel arrays was random, signal gradient had no impact on search behaviour, and individuals did not become more efficient locating the HCF. A separate experiment in which olfactory cues were eliminated by replacing the sugar solution with water was not required on this basis. An elimination test of this nature could have caused the

location of the HCF to be perceived as an unreliable signal by individual birds, and potentially affected the viability of future trials.

Following an encounter with the HCF, bellbirds were able to modify their behaviour and return to the rewarded site with high accuracy across all concentration treatments (85 – 94% accuracy). Post experience adoption of a recursive visitation strategy in the absence of goal-specific cues indicates a spatial memory strategy is being adopted by individuals (Hurly 1996; Mendl et al. 1997; González-Gómez &Vásquez 2006; Perdue et al. 2009; Carter et al. 2010). Conspecific presence did not affect initial array visitation by individuals, or trial performance overall, which suggests that the role of social information was limited within this simple foraging scenario. Conspecifics were also present only in a minority of search and return phase visits, so social information alone would be insufficient to explain the observed behavioural shift.

Performance was largely unaffected by relative value of the higher-quality reward over short time intervals. Return phase accuracy did not significantly vary between the 10, 15, and 20% HCF treatments. These treatments represent the typical range of specialist (15 – 25%) and opportunistic (8 – 12%) bird pollinated plant nectar worldwide (Johnson & Nicholson 2008). The 7% treatment was associated with a slight loss of accuracy, although memory informed search still occurred. It cannot be determined from this study whether the associated drop in accuracy in the 7% trial was due to lower motivation to relocate the HCF or less accurate encoding/recall of the memorised information. There appears to be sufficient benefit gained from adopting memory informed foraging strategies even when the potential improvement is as little as 2% sucrose. These findings suggest that if an individual is motivated to repeatedly return to a plant or flower in a natural system, then the accuracy of recall is unlikely to be compromised by resource quality. For example, the location of an entomophilous or dilute nectar source may be remembered as accurately as ornithophilous sources over short timescales. The availability and perceived value of other alternative resources, such as fruit or invertebrates, may have a greater impact on the expected investment in memory informed

foraging at this temporal scale.

In accordance with the idea that alternative resources could mediate investment in informed foraging behaviours, individuals showed greater investment in sampling behaviour in the low concentration treatment trials (7% and 10% treatments). Sampling allows individuals to monitor and detect improvements in the quality of multiple alternative resources and allocate foraging efforts accordingly (Stephens 2007). Visiting a potentially poor resource imposes a cost of time and energy, investment in sampling behaviour should reflect the potential benefit to be gained as well as the variability of the sampled resource (Hall et al. 2007; Stephens 2007). Resource variability was consistent during the trials, so variation in sampling behaviour is likely due to the greater potential benefit from resource switching in lower-quality HCF trials. As there was no difference between the 15% and 20% treatments I believe that this represents a threshold beyond which sampling offers little benefit.

The measure of sampling used in this trial was conservative and may have underestimated the true level of sampling as it could not include any sampling behaviour that may have occurred prior to visitation to the HCF. The experimental design in this study further favours adoption of a win-stay strategy, i.e. a return to previously rewarded sites. This was deemed appropriate given the spatial and temporal scale of interest to research objectives, but investment in sampling behaviours is likely higher in some foraging scenarios where a win shift strategy is favoured due to potential resource depletion (Burke & Fulham 2003; Sulikowski & Burke 2007).

The effect of resource value on a memory informed search was most pronounced over long timescales. Spatial information from 20% sucrose trials was retained over a period of 20 days, whereas equivalent information in the 10% sucrose trials was not retained, or was retained but not used, over the same interval. The ability to retain information over a 20 day withholding period indicates that bellbirds were capable of forming long term, reference memories (Stephens 2007). At larger spatial and temporal scales, the ability to form long term memories may allow individuals to

make repeated visits to remote natural and artificial resources throughout the flowering period (Spurr et al. 2010). Memory traces persisted for longer intervals when they pertained to higher value rewards, indicating that this information was subject to greater consolidation and maintenance following initial acquisition (Stephens 2007; Fagan et al. 2013). Disparate rates of information decay likely reflect the greater value of information in the high concentration trial (Dall et al. 2005). The risk of forming irrelevant associations and motivation to sample alternative resources may also be higher in the low concentration trials. After a period of 40 days, memories appear to have decayed in both treatments, although providing longer initial exposure and greater reward stability might increase the duration of memory retention. Based on these findings, differential treatment of natural floral rewards is likely over intra-seasonal timescales. Information concerning high value resources, such as ornithophilous typical plant species, e.g. kowhai (*Sophora microphylla*), or flax (*Phormium* spp.), may be retained for the duration of the flowering period or longer, whereas marginal nectar resources, including entomophilous typical species, e.g. five finger (*Pseudopanax arboreus*), may be forgotten once higher quality alternatives have been discovered.

Long term retention of high-value information observed in this study may have more general implications across the avian nectarivore guild. Research on frugivorous and nectivorous primates has concluded that individuals and groups are capable of using long term spatial memory to target out-of-sight, high value, ephemeral resources (Janmaat et al. 2006; Noser & Bryne 2007; Normand & Boesch 2009; Porter & Garber 2013; Janmaat et al. 2013; Ban et al. 2014). Avian nectarivores have also been observed to track resources on a landscape scale, arriving en masse in areas at the onset of resource flowering or immediately prior (Keast 1968; Stewart & Craig 1985; Kuiper et al. 2015; Knowlton et al. 2017). The mechanisms driving these long distance foraging movements in avian nectarivores are poorly understood, but long term retention of high value resources, as identified in this study may be a contributing factor.

The major limitation of this study relates to ecological applicability of findings. Bellbirds forage across a wide range of plant species, experiencing substantial variation in nectar concentration, volume and floral structure (Bergquist 1987; Rasch & Craig 1988; Robertson & Castro 1997; Appendix A). Resource value in these experimental trials has been restricted to manipulation of sucrose concentration as this was straightforward to control in free living trials. In natural systems, the perceived value of natural floral resources could be affected by many factors, including floral abundance, accessibility, nectar volume, rate of replenishment, duration of flowering or patch characteristics. As the results of these trials suggest that investment in memory informed search may be context dependant it will be important for future research to examine these factors in greater detail.

4.6 Conclusions

Resource characteristics likely play a role in mediating investment in informed foraging in this facultative nectarivore species. Small and large increases in the quality of rewards were recalled with similar accuracy over short timescales; however, long term retention appears to be limited to high quality resources. Prior research on memory informed foraging by avian nectarivores has predominantly focused on highly specialised, obligate consumers, with a particular focus on hummingbirds (Henderson et al. 2001; González-Gómez et al. 2011; González-Gómez et al. 2014). These findings highlight that similar processes operate within less specialised systems, and that resource value plays a role in mediating memory-informed foraging processes.

Chapter 5

Visual cue use during foraging by New Zealand bellbirds (*Anthornis melanura*)

5.1 Abstract

Foragers use a variety of cues to locate resources within their foraging environments. Bellbirds (*Anthornis melanura*) have previously been shown to use spatial cues to revisit high value resources. Other sources of information, such as visual cues, have not been examined but may be important drivers of foraging behaviour. Free-living bellbirds were trained to associate the presence of a visual cue at an experimental feeder with the availability of a high concentration sugar water rewards (20% sucrose). Un-cued experimental feeders always contained low concentration sugar water (5% sucrose). Over the course of the experimental period individuals learnt to utilise the visual cue in novel environments. Utilisation increased with trial experience; initially 42% of birds utilised the available cue, but after two prior exposures, 89% of birds utilised information provided by the cue. Once birds had learnt the association between reward characteristics and the presence of a visual cue, mixed cue trials were performed in which participants could rely on either previously acquired spatial information, or the visual cue. Bellbirds largely demonstrated spatial priority in the mixed cue trials – this is typical of many other specialist nectivorous foragers.

5.2 Introduction

Foragers always face uncertainty when locating resources in natural environments (Stephens 2007). Resource quality and availability vary according to multiple spatiotemporal scales and such variability can be further exacerbated by stochastic events (Stephens 2007). The ability of foragers to utilise external cues to locate and remember high quality food resources reduces the amount of uncertainty they face and allows for more efficient resource acquisition (Dall et al. 2005). Natural environments provide many potential cues, e.g. olfactory, visual, gustatory, auditory, and spatial, but these cues vary in terms of their precision and stability (Dall et al. 2005). The type of cue which is most informative is dependent on the foraging context.

Two cues that are often examined within the context of avian nectarivores are spatial and visual cues. The acquisition and retention of spatial information is important for nectarivores due to the depletable but renewable nature of floral nectar (Berger-Tal & Bar-David 2015). Spatial memory allows individuals to return to rewarding sites across a variety of timescales and to avoid depleted resources (Hurly & Healy 1996; Burke & Fulham 2003; Henderson et al. 2006). Hummingbirds (Trochilidae) are the most morphologically and behaviourally specialised family of avian nectarivores (Pyke 1980; Fleming & Muchhala 2007; Nicholson & Fleming 2014). Specialisation for nectar feeding has selected for exceptional spatial memory abilities in this family (Ward et al. 2012). Hummingbirds have been shown to remember the location of individual flowers (Hurly & Healy 1996; Henderson et al. 2001; González-Gómez & Vásquez 2006) and associate this with variation in quality (Bateson et al. 2003) and rate of replenishment (Henderson et al. 2006). Spatial memory has also been studied to a lesser extent in sunbirds (Nectariniidae) and honeyeaters (Meliphagidae) which are less specialised avian nectarivores (Gill & Wolf 1977; Burke & Fulham 2003; Sulikowski & Burke 2010; Chapter 4).

Flowers provide many visual cues for use by pollinators, including shape, size and colour (Raguso 2004). Foragers that are capable of associating these visual cues with rewards are often able to

forage more efficiently. Flower colour is a highly conspicuous cue and plays an important role in flower choice of visually orientated pollinators (Cronk & Ojeda 2008; Handelman & Kohn 2012; Shrestha et al. 2013; Dötterl et al. 2014; Cepero et al. 2015). Nectar feeding birds have been shown to respond to floral colour in observational studies (Scoble & & Clarke 2006) and form associations between colour cues and reward availability under experimental conditions (Meléndez-Ackerman et al. 1997; Sandlin 2000; Hurly & Healy 2002; Whitfield et al. 2013; Sulikowski & Burke 2015). Hummingbirds have been shown to associate colour cues with variation in reward quality (Bateson et al. 2003) and refill rate (Samuels et al. 2014).

Natural environments present many potential cues to foraging animals simultaneously. Although cue integration may occur in some contexts (Collett & Kelber 1988), in most situations the presence of multiple cues leads to competition for behavioural control (Stephens 2007). Salient, or biologically significant, cues are generally less susceptible to cue competition (Denniston et al. 1996). In cases where hummingbirds are presented with both visual and spatial cues, visual cues are usually disregarded in favour of spatial information (Hurly & Healy 1996; Hurly & Healy 2002; Tello-Ramos et al. 2014). Visual cues are typically only prioritised in novel environments where prior spatial information is unavailable (Hurly & Healy 1996), or in changeable environments in which prior spatial information becomes unreliable (Flores-Abreu et al. 2012).

Spatial priority in hummingbirds may reflect higher resolution of information offered by spatial cues, as visually identical flowers can vary in terms of reward quality, both between and within plants (Marshall et al. 2012). Cue competition between spatial and visual cues has not been widely examined among families of avian nectarivores outside of the hummingbirds. Franks & Thorogood (2018) examined spatial and visual cue use in a less specialised nectarivore species, the New Zealand hihi (*Notiomystis cincta*), and found a much greater attendance to visual cues relative to spatial cues than has previously been reported. Individuals were presented with a colour cued reward over a period of five days. When the reward positions were altered, initial selections were fairly evenly

distributed between prior location (44.4%) and colour cued (38.8%) sites (Franks & Thorogood 2018).

The purpose of this study was to examine the use of visual cues by bellbirds (korimako, *Anthornis melanura*) which are also native to New Zealand (Heather & Robertson 2015). Bellbirds belong to the honeyeater family and bear morphological adaptations to nectar feeding, including a decurved bill and protrusile, bristle tipped tongue (Heather & Robertson 2015). Like other honeyeaters they occupy a generalist feeding niche. Although bellbirds preferentially feed on nectar, they will switch to a predominantly invertebrate or fruit-based diet when nectar is not available (Craig 1985; Murphy & Kelly 2003). Observational studies by Delph & Lively (1985) suggested that bellbirds preferentially visited *Fuchsia excorticata* according to the colour stages of individual flowers, indicating some use of visual cues at a fine scale. I, therefore, expected that bellbirds would be capable of forming a learned association between the presence of a visual cue and a reward. Recent work has demonstrated that bellbirds can use spatial memory to relocate nectar rewards (Chapter 4). I examined the use of visual cues both in the presence and absence of prior spatial information in order to determine whether cue utilisation was affected by prior experience and cue competition. I expected that bellbirds would demonstrate spatial priority with regard to cue use – due to facing similar selection pressures for nectar foraging as hummingbird species (Hurly & Healy 2002; Tello-Ramos et al. 2014).

Hypotheses:

1. I expected that, after appropriate training, bellbirds' initial feeder choices within a novel experimental array would be non-random in the presence of a conspicuous visual cue. Previous research has shown that bellbirds forage randomly in novel arrays when a visual cue is not provided [Chapter 4], therefore, non-random foraging would be indicative of cue utilisation.

2. I also expected that, in cases where foragers had prior experience of an array, individuals would preferentially return to a historically rewarded feeder, rather than a feeder that was visually cued. Preference for a historically rewarding feeder, when visual and spatial cues were presented in conflict, would demonstrate priority of spatial information.

5.3 Methodology

Experimental methodology described in this study is similar to that in Chapter 4 which examined spatial memory in the absence of visual cues.

5.3.1 Study subjects

Feeder trials were conducted in Takamatua, a coastal settlement within the Akaroa Harbour, Canterbury, New Zealand (42.79'S, 172.96'E). The local landscape is a mosaic of residential properties, patches of native forest, and farmland. Bellbirds are present in the area throughout the year, although the population experiences seasonal variation in numbers. Free living bellbirds in the area had prior experience using sugar-water feeders as many local residents engage in supplementary feeding. Banded individuals have been observed to make repeated visits to feeders both within and between years (G. Bedford pers. obs.). Adult male bellbirds were banded at supplementary feeding stations prior to the trials to allow for individual identification. Female bellbirds were not included in this study as they were infrequent visitors to feeders at this site (J. Dent pers. obs.). The study took place between May and July of 2017. Individuals were not territorial at this time and aggression at the feeder array was rare which allowed multiple individuals to utilise the experimental array simultaneously. Memory informed foraging trials [Chapter 4] had previously been conducted at the Takamatua location; these trials were halted prior to visual cue training and did not resume for the duration of the experimental period. Of 27 individuals that participated in visual cue trials, 18 had previously participated in memory-informed foraging trials [Chapter 4].

5.3.2 Experimental design

Training period

Prior to this study, subjects were trained to use experimental feeders. Feeders consisted of a 1 litre reservoir of sugar water which emptied into a small feeding dish. Each feeder and a 20 cm perch were mounted on a free standing stake measuring 1.6 m in height. During visual cue training, four experimental feeders were erected throughout the experimental site. Two feeders contained high concentration sugar water (20% sucrose) and two feeders contained low concentration sugar water (5% sucrose). The high concentration feeders were signalled by the addition of a colourful visual cue; a yellow disc mounted on the sugar water reservoir. This was thought to be an appropriately conspicuous visual cue due to the violet-sensitive vision system of honeyeaters (Hart 2001; Ödeen & Håstad 2010). The purpose of this trial was not to determine a bellbird's ability to associate a particular colour with a reward; rather it was to determine whether they could learn to associate the presence or absence of a conspicuous visual cue with reward quality. Training lasted for 16 days, and on two occasions during the training period the location of all feeders were changed to avoid formation of spatial biases. The long duration of the training period was necessary to ensure sufficient exposure of the free living study subjects to training feeders as there was large variation in individual visitation rates. All 27 study bellbirds visited the experimental site on multiple days during the training period (3+ days). Training each individual to a specified criterion was not possible due to the free-living nature of the experimental trials.

Experiment 1: Cue utilisation

A 1 m x 1 m square array consisting of four identical feeders was established in a novel location (3 m clearance from other experimental or training sites) (Figure 14). Three of the feeders were supplied with 1 litre of low concentration sugar water (5% sucrose) while the remaining feeder was supplied with 1 litre of high concentration sugar water (20% sucrose) (Figure 14). The location of the high

concentration feeder was randomly determined and was signalled with the visual cue used during the training period (Figure 14). Birds were allowed to visit the array freely for a period of 48 hours. During this time, daytime visitation to the array was monitored by two cameras (Ltl Acorn 5310A model) at opposite ends of the feeding array which recorded time-lapse images at a rate of two images at two seconds intervals [as per Chapter 4]. Direct observation at the start of each experiment was used to confirm the accuracy of this data collection approach. If feeders were emptied throughout the course of the experiment the reservoir was refilled at the appropriate concentration. Four experiments of this type were conducted at approximately weekly intervals (7 – 10 days), each in a novel location to avoid spatial bias. Trials were only conducted in fine weather to prevent dilution of sugar water by rainfall.

Individual visitation was categorised into two phases; search and return phases. The search phase visitation included all visits to experimental feeders up to and including the first interaction with the high concentration feeder. All subsequent feeder visits were classed as the return phase. In some instances individuals visited multiple feeders in rapid succession. Visits were considered part of the same visitation bout if they were separated by a period of less than 5 minutes. A return phase bout was considered successful if the first re-visit to the array was to the high concentration feeder.

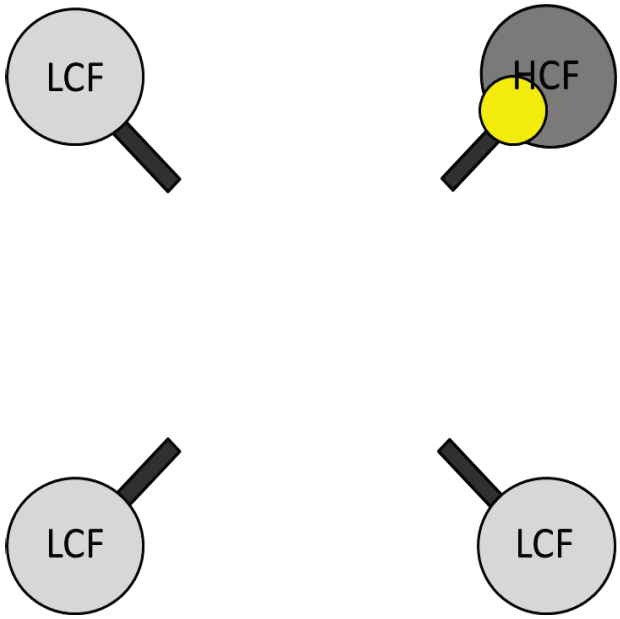

Figure 14: Experimental array used in Experiment 1 [visual cue learning]. The location of the high concentration feeder is signalled by a yellow disc which acted as a conspicuous visual cue.

Experiment 2: Multiple cue response

As in Experiment 1, a four feeder array was established, although no visual cue was provided to signal the location of the high concentration feeder (Figure 15). Birds visited the array for a period of 24 hrs. In most cases this duration was sufficient to allow individuals to sample the array and locate the high reward feeder (Phase 1). After 24 hrs, the feeders were emptied until the following morning (approximately 20 hr withholding period). Following the withholding period, both the originally rewarded feeder and the diagonally opposite feeder were filled with high concentration sugar water (20% sucrose) (Figure 15). The newly rewarding feeder was signalled with the visual cue previously employed in Experiment 1 while the originally rewarding feeder remained un-cued (Phase 2; Figure 15). Subsequent visitation by banded individuals was then recorded for a further 24 hours, or until the sugar water supply was depleted.

The first visit of phase 2 was categorised as either ‘spatial’ (return to originally rewarding feeder), ‘visual’ (return to visually cued feeder) or ‘other’ (return to low concentration feeder) (Figure 15). Participants were required to visit the high concentration feeder at least once during phase 1 to be considered during phase 2. Two mixed cue trials were performed in novel locations to maximise the number of participants exposed to at least one mixed trial.

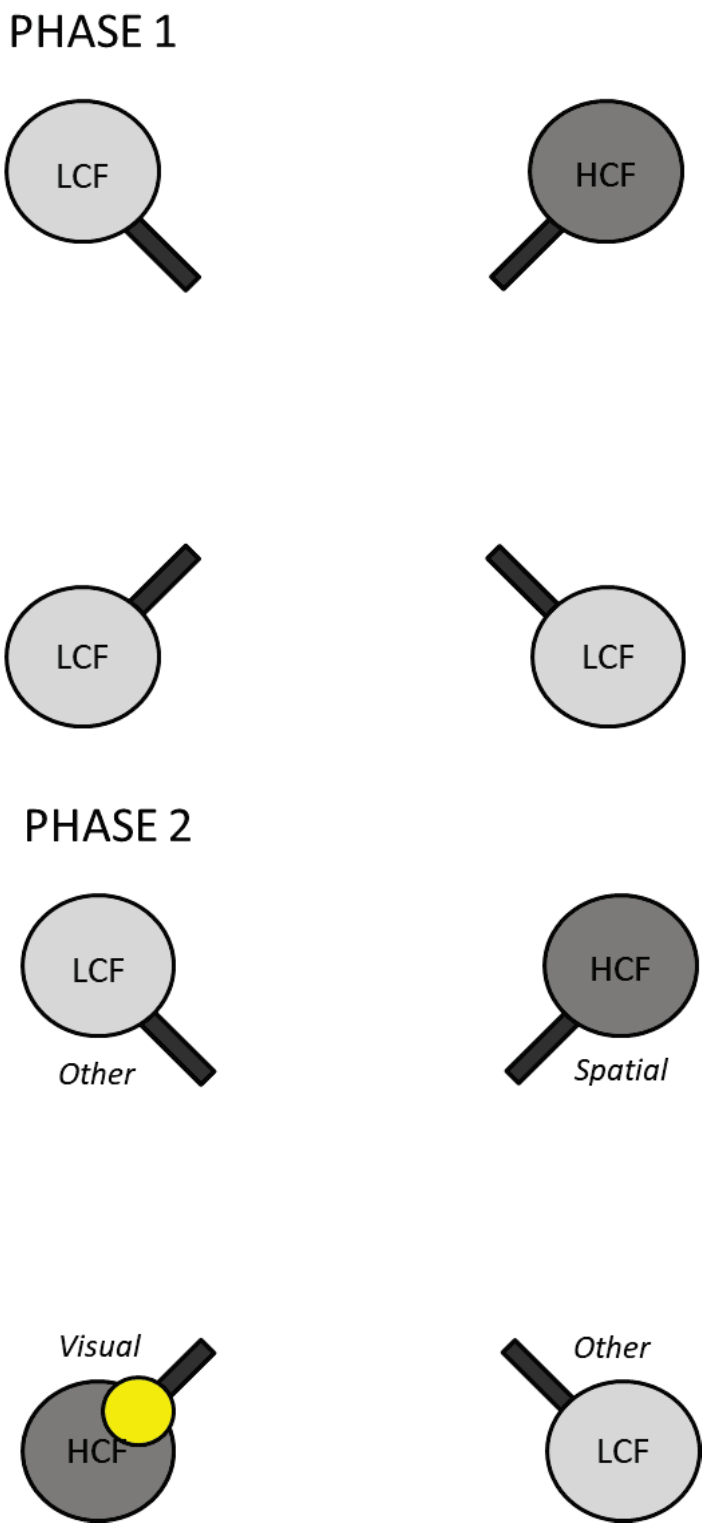

Figure 15: Experimental array used in Phase 1 and Phase 2 of Experiment 2 [multiple cue]. All high concentration feeders [HCF] contain 20% sucrose; low concentration feeders [LCF] contain 5% sucrose. Visitation strategy in Phase 2 was defined as either “Visual”, “Spatial” or “Other”.

5.4 Statistical analysis

Data was analysed using SPSS version 20 (IBM Corp. 2011).

Experiment 1: Cue utilisation

Performance in visually cued trials was compared to the performance expected from random foraging in a series of one sample t-tests. Search phase visitation (number of feeder visits performed before visiting visually cued HCF) was compared to the median number of visits expected in a random foraging scenario (2.4, based on the geometric random distribution). Return phase visitation (proportion of bouts in which the initial encounter was with the visually cued HCF) was compared to the proportion of visits expected if feeders were visited equally (0.25). Data from each trial was analysed separately to account for the possibility that the strength of the visual association might increase over time.

In each trial the first search phase visit was indicative of whether an individual had utilised the visual cue or not. To determine if cue utilisation increased with individual experience I modelled a generalised estimating equation (GEE) with a binomial error structure and logit link function. GEE are similar to generalised linear models but allow for repeated measures. Three predictor variables were included in the model: experience, conspecific presence, and an interaction term. The experience term was a repeated measure with up to three levels per individual (1st trial, 2nd trial, 3rd trial). Only the first three experience levels were analysed due to insufficient representation in the four trial group. Conspecific presence indicated that conspecifics had fed from the array within 30 seconds of the focal birds approach. Post hoc reverse Helmert contrasts were performed for significant predictor variables.

Experiment 2: Mixed cue

Only individuals that utilised visual cues in experiment 1 were considered in the analysis of the mixed cue trials. A binomial test was performed to determine if there was a bias towards either the "visual" or "spatial" response. If both responses were equally favoured the probability of choosing either would be 0.5. Only the first exposure of each individual was included in this test.

5.5 Results

A total of 27 individuals participated in cue utilisation trials. Individuals performed fewer search phase visits, and returned to the high concentration feeder, with higher accuracy than expected by chance across all cue utilisation trials (Table 4).

Table 4: One sample t-test results for search phase visitation and return phase accuracy. Trial results were compared to values expected from random visitation (2.4 search phase visits, 25% accuracy of return bout visits). Significant values at $\alpha = 0.05$ level are indicated by *.

	Search phase visitation			Return phase accuracy		
Trial	Mean	df	P	Mean	df	P
1	1.83	11	0.038*	0.96	11	<0.001*
2	1.64	17	0.005*	0.95	17	<0.001*
3	1.51	17	<0.001*	0.95	17	<0.001*
4	1.08	12	<0.001*	0.96	12	<0.001*

Initial visitation to the high reward feeder occurred more often than expected by chance (25%) across all experience groupings (Figure 16). The GEE indicated that previous trial experience was a

significant predictor of cue utilisation (Wald X^2_2= 8.86, p = 0.012). Cue utilisation by birds in their second experience of cued trials (75%) was greater than for birds in their first experience (42%) (Wald X^2_1 = 4.2, p = 0.039) (Figure 16). Utilisation in the third experience grouping (89%) was greater than for both prior groupings combined (Wald X^2_1 = 8.7, p = 0.003) (Figure 16). Conspecifics were present in 41% of first visits to experimental arrays. Cue utilisation during the first visit was not affected by the presence of conspecifics (Wald X^2_2 = 0.53, p = 0.77) nor by the interaction between conspecific presence and individual experience (Wald X^2_1 = 0.10, p = 0.75). The interaction between experience and age was not examined due to the unbalanced age structure of the sample population. Only five first year birds were included in the study, while the remainder were second-year or older.

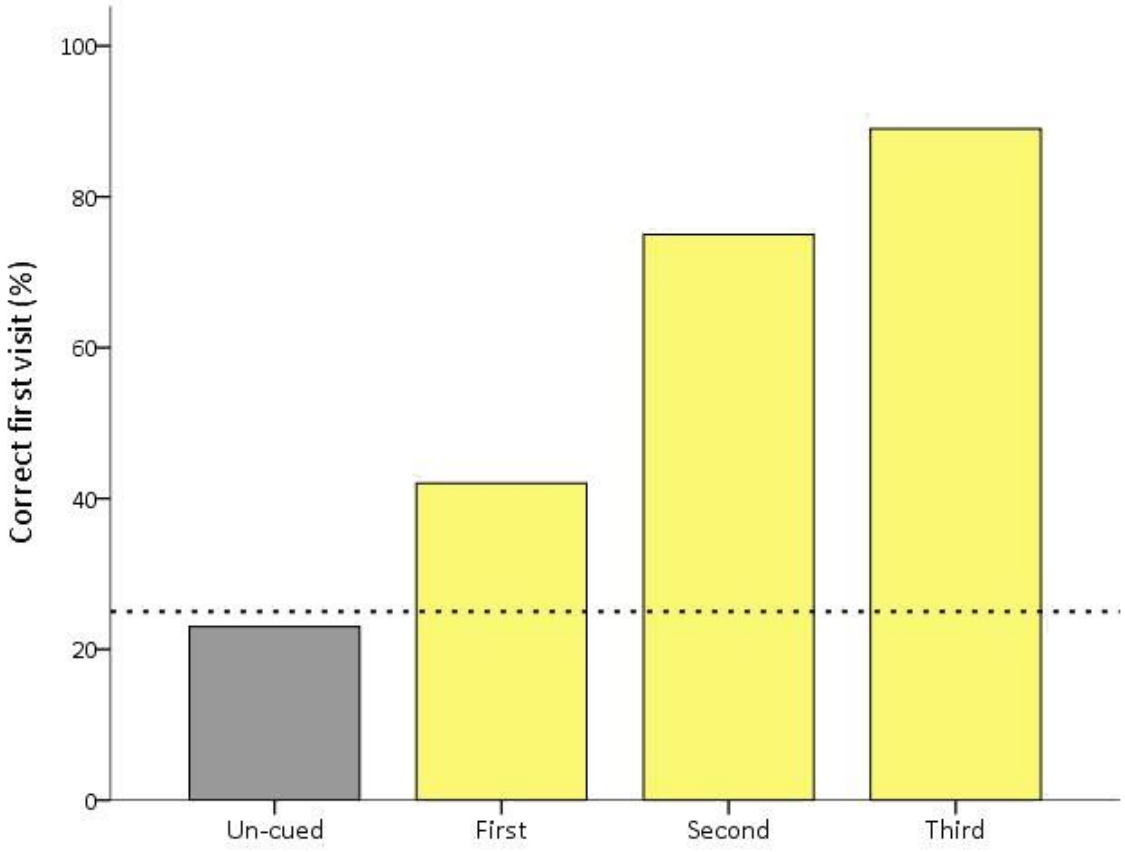

Figure 16: Initial visit success of bellbirds feeding from experimental arrays after visual cue training (first, second and third visual trial experience; yellow bars). The grey bar depicts initial visit success in separate, un-cued trials which were conducted as part of Chapter 4 [20% sucrose treatment]. Dashed line represents the percentage of correct feeder selection expected by random foraging (25%).

Of the 27 individuals that participated in the utilisation trials, 24 demonstrated successful utilisation of a visual cue in at least one of the four trials. Nineteen of these individuals were then present in a mixed-cue trial. All first responses during phase 2 were to the visual (1/19, 5.3%), or the spatial (18/19, 94.7%) feeder. The binomial test confirmed a preference for the spatial feeder over the visual feeder ($p < 0.001$). In six cases, birds trained on visual cues did not visit the array during phase 1 but were present during phase 2 and presumably lacked prior spatial knowledge. For these individuals the phase 2 visit would have been equivalent to encountering a new visually-cued array. In all of these cases the visual cue feeder was the first visited.

5.6 Discussion

In the presence of a visual cue, bellbirds visiting an experimental array foraged more efficiently than expected by chance. Individuals required fewer visits to locate a high quality feeder than would be anticipated in a random or un-cued [as in Chapter 4] foraging scenario. As experimental feeders were indistinguishable, and individuals had no prior spatial knowledge of the array, this non-random search behaviour can be attributed to a learnt association between the presence of the visual cue and high concentration sugar water. Olfaction has not been shown to drive search behaviour in bellbirds [Chapter 4], or in any other species of avian nectarivore, so is unlikely be a driver of the observed behaviour. Furthermore, if olfaction was driving search behaviour in these experiments, rather than visual or spatial information, then visitation in phase 2 of the mixed-cue trials would have been evenly split between the two HCF feeders. Social cues may have aided in the acquisition of the relevant visual association (Jones et al. 2013; Davis & Burghardt 2011) but could not solely account for the observed utilisation. The majority of initial encounters with the experimental arrays were performed in the absence of conspecifics, and conspecific presence did not affect the likelihood of success. The ability of bellbirds to use visual cues to increase efficiency in novel environments is consistent with prior research on avian nectarivores, including rufous hummingbirds (*Selasphorus rufus*) (Hurly & Healy 2002) and amethyst sunbirds (*Chalcomitra amethystine*) (Whitfield et al. 2014).

Bellbirds also foraged non-randomly during the return phase of visual cue utilisation trials. During the return phase, it cannot be determined if observed recursive visitation was driven by the continued use of a visual cue [as in search phase] or by newly acquired spatial information [Chapter 4]. Return performance observed in visual cue utilisation trials (95 – 96% accuracy) was consistent with that observed in comparable 20% sucrose, un-cued trials performed in Chapter 4 (95% accuracy). Information is only valuable when it beneficially modified the behaviour of the forager (Dall et al. 2005). I speculate that visual information is of less value to foragers when making return

visits to the experimental array than during the initial array encounter. This was supported by the results of the mixed-cue experiment, in which birds preferentially returned to the spatial location of a known high-reward feeder, rather than a visually-cued high-reward feeder.

Context dependent variation in cue value may have implications for bellbird foraging behaviour at a seasonal scale. Bellbirds are territorial during their breeding season which extends from late spring to mid-summer (October - January) (Anderson & Craig 2003), often returning to the same breeding areas between years (Anderson & Craig 2003; Brunton et al. 2008b). Outside of the breeding season, bellbirds are solitary and disperse over greater distances (Heather & Robertson 2015; Chapter 3). Colour or other visual cues are likely to be most important during this period of nomadic foraging as birds, particularly first-year birds, are more likely to be encountering novel environments where they do not have a pre-existing spatial reference. The nomadic period, which spans most of the year from late summer to early spring, coincides with onset of flowering in several key native sources of nectar, e.g. kowhai (*Sophora microphylla*), tree fuchsia (*Fuchsia excorticata*), puriri (*Vitex lucens*), toropapa (*Alseuosmia macrophylla*) and climbing rata (*Metrosideros fulgens*), all of which produce colourful flowers that could function as visual cues (Delph & Lively 1985; Newstrom & Robertson 2005; Spurr et al. 2011; Dawson & Lucas 2012; Heather & Robertson 2015). Exotic sources of nectar, such as winter flowering gum (*Eucalyptus* spp.) and *Banksia* spp., also produce colourful floral displays during this time (Spurr et al. 2014; Heather & Robertson 2015). Once birds have located key resources, or established territories during the breeding season, visual cues are expected to become less important as birds can utilise prior knowledge of spatial locations to accurately return to high quality sites. Visual cues may still play a role during extra-territorial forays and in signalling the onset of flowering in known resources.

The association between a visual cue and reward value was learned gradually throughout the trial process. In the first experience of a cued trial after training, only 42% of individuals initially utilised visual cues, although this increased to 89% by the third experience. Utilisation in the first experience

group was lower than expected based on prior research. Hummingbirds and sunbirds are known to readily acquire visual associations, often within a matter of hours (Goldsmith & Goldsmith 1979; Meléndez-Ackerman et al. 1997; Pérez et al. 2011; Whitfield et al. 2014). Some individuals have been reported to learn a visual association after just one experience (Goldsmith & Goldsmith 1979; Sandlin 1999), and those that do not, typically learn within two - three experiences (Hurly & Healy 1996; Sandlin 1999). In experiment 1, the majority of bellbirds (58%) did not utilise visual cues after 16 days of cue training. Further experience in a trial context was required to facilitate cue utilisation on the scale observed in hummingbirds (Goldsmith & Goldsmith 1979; Hurly & Healy 1996; Sandlin 1999; Pérez et al. 2011). Though they formed slowly, once associations had been learned they were maintained between trials that were 7 - 12 days apart.

There are two potential explanations for the delayed formation of associative memories in this study. First, the free living nature of the trial population may have reduced the effectiveness of the visual cue training as availability of alternative resources may have reduced motivation to learn visual associations (Balkenius & Bulkenius 2010). Laboratory based studies or studies with highly territorial subjects are likely to have fewer competing stimuli during training (Balkenius & Bulkenius 2010). Second, slower formation of associative memories may reflect the natural conditions under which bellbirds forage. Ornithophilous-type flowers, with conspicuous colourisation, occur in just 11 genera of native New Zealand plants (Newstrom & Robertson 2005). Nectar from small, inconspicuous or entomophilous-type flowers also forms a significant part of the bellbird diet (Godley 1979; Castro & Robertson 1997). Relevance of cues within the local environment is known to affect cue learning and memory both within and between species (Braithwaite & Guilford 1995; Girvan & Braithwaite 1998; Couvillion et al. 2010). Girvan & Braithwaite (1998) determined that three-spined stickleback (*Gasterosteus aculeatus*) populations that inhabited river environments were less capable of using visual cues in experimental trials than populations that inhabited pond environments where visual cues are more stable. Low prevalence of informative, conspicuous visual signals in the native New Zealand environment may indicate that visual cues lack the environmental

relevance they have in other nectarivore systems, and contribute to slow formation of visual associations in this species. Replication of cue utilisation trials, with greater control over training experience, and with inclusion of other New Zealand nectarivores, such as the more nectivorous tūī, would allow examination of this trend in greater detail.

Second, as demonstrated in the mixed-cue trials, in the face of conflicting cue information, spatial information was prioritised over visual cues. Similar overshadowing of spatial information over visual cues has also been described in hummingbirds (Hurly & Healy 1996; Tello-Ramos et al. 2014) as well as in food storing parids (Brodbeck 1994) and corvids (Clayton & Krebs 1994). Spatial priority in these species, as in bellbirds, likely reflects the high value of accurate, recursive visitation in their respective foraging contexts. It is interesting that results of this study are in contrast with a recent study on cues used by the New Zealand hihi (Franks & Thorogood 2018), as bellbirds and hihi occupy a similar foraging niche (Craig et al. 1981; Heather & Robertson 2015). Franks & Thorogood (2018) found that adult hihi initially responded almost equally to spatial (44.4%) and visual cues (38.8%) when they were presented in conflict, a result similar to that described for non-storing parid and corvid species (Brodbeck 1994; Clayton & Krebs 1994). Differential prioritisation of cues could result from methodological differences between studies. For example, many of the bellbirds that participated in this study had previously participated in trials that provided high-concentration rewards at a stable location [Chapter 4], which may have encouraged reliance on spatial cues. Additionally, Franks & Thorogood (2018) conducted trials at a much smaller spatial scale (c. 5 cm between rewards) which may have affected the type of spatial information acquired (Healy & Hurly 1998). Variation in the value of visual and spatial cues may also result from the dominance hierarchy among New Zealand nectarivores which sees hihi excluded from high quality nectar sites (Rasch & Craig 1988). Hihi occupy a more marginalised nectar feeding habit than bellbirds which may limit the value of recursive visitation. It would be beneficial to study these two species, as well as tūī, under more equivalent conditions to determine whether differences in cue use between these similar species are methodological or behavioural in nature.

As this is the first study to examine visual cue use by bellbirds, experimental trials were designed around simplistic use of visual cues. The presence or absence of a conspicuous visual cue was a reliable indicator of reward value in all cases. This form of cue utilisation is useful in some contexts, e.g. identifying a flowering tree within the foraging environment, but limited in others, e.g. distinguishing flowers within an inflorescence. Future research should focus on utilisation of more precise visual information, such as specific colours, markings or shapes, which may be more important at smaller foraging scales. It may also be important to examine whether cue utilisation and priority vary on a seasonal basis, e.g. breeding vs. non-breeding season, or with regard to demographics, e.g. age or sex variation.

5.7 Conclusion

New Zealand bellbirds were capable of forming visual associations to locate nectar rewards. The rate of learning appeared slower than observed in other avian nectarivore systems. However, once associations were formed, they were similarly accurate and long lasting. Like highly specialist nectarivores and seed caching species, bellbirds demonstrated spatial priority in cases of spatial and visual cue conflict. Prior research on cue use in specialist nectarivores has largely focused on hummingbird species. This study emphasises the need to consider the role of variable environmental relevance, and interspecific variation, in cue learning and memory.

Chapter 6

Scale dependant use of relative and absolute spatial cues in foraging bellbirds (*Anthornis melanura*): a pilot study

6.1 Abstract

Foragers often use external features of the environment to relocate resources. The use of relative and absolute spatial cues by free-living New Zealand bellbirds (*Anthornis melanura*) was examined in the context of visitation to an experimental feeder array. Four trials were conducted in this pilot study. In each trial, four sugar water feeders were presented in a square configuration. The size of the array was modified between trials. Initially individuals learnt the location of a single high concentration feeder. After initial spatial learning, the array was displaced sideways. In the new arrangement, individuals had a choice of either returning to the absolute spatial position, or the relative spatial position of the original high concentration feeder. An absolute spatial strategy was favoured in the largest arrays (70 cm, 85 cm, 100 cm), while a relative strategy was favoured in the smallest array (55 cm). These results suggest that bellbirds learned and remembered the absolute, rather than relative, positions of high-quality feeders in other experiments. They also provide a basis for further study of visual cue use by bellbirds.

6.2 Introduction

Spatial memory, in various forms, is used to encode, store and retrieve spatial information across a variety of animal taxa (Healy & Hurly 1998; Thiele & Winter 2005; Vlasak 2006; Fukumori et al. 2010; Guigueno et al. 2014; Stephan et al. 2015). The ability to return to, or avoid, familiar locations often confers a fitness benefit (Fagan et al. 2013). At local scales, spatial memory allows a larger choice of locations for feeding, nesting or hiding (Henry & Stoner 2011; Guigueno et al. 2014; Maille & Schradin 2016). Spatial memory may also allow for better predictions about the location of predators or conspecifics (Schwagmeyer 1994; Stephan et al. 2015). At larger scales, spatial memory allows for more efficient navigation in complex environments (Porter & Garber 2013) and for the relocation to key sites, such as breeding grounds (Fukumori et al. 2010; López-López et al. 2014) or intermittently available resources (Janmaat et al. 2013).

Spatial information is acquired and utilised using a variety of different cognitive strategies (Stephens 2007). As spatial information is always relative, stored spatial representations must have a frame of reference (Adams-Hunt & Jacobs 2007). Frames of reference are allocentric or egocentric in nature (Burgess 2006). Allocentric spatial information is coded relative to external cues, e.g. a location is 10 m south of a nest (Burgess 2006). Egocentric spatial information encodes locations relative to internal, movement based cues, e.g. a food source is 20 m to an individual's right (Burgess 2006). The content of a spatial representation can range in complexity from simple (e.g. beacon or dead reckoning), to highly complex and integrated (e.g. cognitive map) (Adams-Hunt & Jacobs 2007). Spatial strategies do not exist in isolation. Multiple representations of objects in space are acquired simultaneously and successful navigation requires an ability to combine or switch between different reference frames (Burgess 2006; Odling-Smee et al. 2008). Species vary in regard to their reliance on different spatial representations due to variation in navigational requirements (Clayton & Krebs 1994), and perceptual limitations (de Perera 2004). Environmental conditions can also limit the efficacy of different spatial representations in some contexts (White & Brown 2015).

New Zealand bellbirds (*Anthornis melanura*) use spatial memory during foraging (Chapter 4). Individuals can learn the location of a high quality resource within an experimental array after a single encounter (Chapter 4). In a natural environment, spatial memory likely enables bellbirds to remember and return to high value resources which are scattered throughout their foraging range, whether natural or human-modified. It is currently unknown which spatial cues are most important to bellbirds during memory informed foraging. Many studies have demonstrated that birds typically rely on external landmarks to re-locate food rewards in familiar environments (Gould-Beiele & Kamil 1998; Mora et al. 2012; Hurly et al. 2014). Research on the use of landmarks has largely been conducted under controlled laboratory conditions that do not always translate to natural conditions and increasing emphasis is being placed on conducting cognitive research in more realistic, field based studies (Pritchard et al. 2016). Though more applicable to natural behaviours, field studies of spatial cue use can be complicated by the enormous number of potential landmarks that individuals can use for orientation (Pritchard et al. 2016).

Landmarks are broadly divided into two classes; local or global cues. Local cues are those provided by objects close to a goal (e.g. a nest, flower, or rock), or by the goal itself. Typically local cues provide information about the relative position of a goal with respect to nearby features (Vlasak 2006; Legge et al. 2009). Global cues are provided by objects located further from the goal, or by environmental features, such as forest edges and landscape relief. Global cues usually provide information about the absolute location of a goal (Vlasak 2006; Legge et al. 2009). Use of landmarks varies greatly across species, task types and environments (Cheng & Spetch 1998). In most situations, there is a degree of redundancy in landmark use and cues often vary in their relative importance (Legge et al. 2009). Many avian studies have shown preferential use of global landmark features (Brodbeck 1994; Gould-Beierle & Kamil 1996; Legge et al. 2009; Flores-Abreau et al. 2012) but local cues are favoured in other contexts where they may provide additional precision and accuracy (Cheng 1989; Bennet 1993; Legge et al. 2009). The aim of this pilot study was to examine whether bellbirds carrying out a spatial memory task appeared to remember the absolute position

or relative position of a high-reward feeder, across a variety of experimental scales. If birds appeared to remember the relative position, this would suggest they predominantly used local (intra-array) cues. If birds remembered the absolute location, this would suggest they relied more on global (external to the array) cues. This pilot study will ensure that future research on landmark use by bellbirds is conducted at an appropriate scale, as well as providing insight into the mechanisms driving the memory informed foraging behaviours reported in previous chapters [Chapter 4 & 5].

Hypotheses:

1. Bellbirds foraging within displaced experimental arrays will preferentially visit the feeder occupying the absolute spatial position of a previous reward, rather than the feeder occupying the equivalent relative position within an array. This preference for absolute spatial strategy would be indicative of greater salience of global cues (external to the array arrangement) that are unaffected by the array displacement.

   Preferential return to the absolute, rather than relative, position of the rewarding feeder will persist across multiple array sizes.

6.3 Methodology

6.3.1 Study subjects

Experimental trials were conducted in Takamatua, Banks Peninsula, New Zealand (42.79'S, 172.96'E). Twenty nine, banded adult male bellbirds participated in the trials. All subjects had previously participated in cognition trials (Chapter 4 and Chapter 5), and were familiar with the use of experimental feeders. The study took place between November and December of 2017, which coincided with the bellbird breeding season. Although bellbirds are often territorial during this time,

experimental sites were positioned in locations where they were not defended by dominant individuals (J. Dent, pers. obs.).

6.3.2 Experimental design

Experimental feeders consisted of a 1 L reservoir which emptied into a round feeding dish. Feeders and 20 cm perches were suspended on free standing stakes measuring 1.6 m in height. Initially, four experimental feeders were presented in a square array (Figure 17, Phase 1). One randomly determined feeder was supplied with sugar water at a concentration of 15% sucrose; the other three feeders contained a lower concentration of 5% sucrose. Four trials were conducted; each with a unique distance between feeders of 55 cm, 70 cm, 80 cm, or 100 cm (Figure 17). Trials were performed in a random order and each was conducted at a unique location within the study site. All feeders had a clearance of at least 1 m from surrounding vegetation.

Bellbirds were allowed to visit the array freely for a period of 48 hours in order to learn the location of the high concentration feeder (Chapter 4). The array was then transposed sideways relative to the high reward feeder by a distance of one feeder spacing (Figure 17, Phase 2). This manipulation changed the local (intra-array) cues indicating the relative position of the original high-reward feeder, while leaving the global (external to the array) cues indicating the absolute position of the original high-reward feeder unchanged. Both the feeder occupying the absolute location of the high concentration feeder during training (Figure 17: Phase 2, Feeder C) and the feeder occupying the relative intra-array position of the training feeder (Figure 17: Phase 2, Feeder E) were supplied with 15% sugar water following the feeder displacement to avoid negative associative learning. Bellbirds continued to visit the array for a further 48 hours. Visitation to the array was assessed via continuous time-lapse imagery (two images every 2 seconds) collected from two Ltl Acorn cameras (5310A), situated at opposite ends of the array, in addition to periods of direct observation. During direct observation, individuals were not observed to approach the arrays from consistent directions

so egocentric information, if present, was expected to be secondary to allocentric information use (J. Dent pers. obs.).

6.3.3 Statistical analysis

Individuals were required to visit the high concentration feeder in the original array (Phase 1) a minimum of five times to be considered for analysis after displacement during Phase 2 (Chapter 2). The first feeder visited after displacement was assumed to be indicative of spatial cue preference during initial learning. Visitation to the original reward feeder's absolute location (Figure 17, Feeder C) was categorised as "absolute strategy", visitation to the original reward feeder's relative position in the array (Figure 17, Feeder E) was categorised as "relative strategy", and visitation to the low concentration feeders was categorised as "other" (Figure 17).

Binomial tests were performed to determine if there was a bias towards "absolute" or "relative" strategies in the initial responses to Phase 2 of each experimental trial. Each response was compared to the probability of randomly choosing the feeder from a four feeder array (0.25). A generalised estimating equation (GEE) with a binomial error structure and logit link function determined whether the strategy choice was related to array size. Array size was included as the predictor variable. Array size was a repeated measure in some cases because the majority of individuals were present in multiple trials. Only cases where the "absolute" or "relative" feeder were initially visited were included in this model. Orthogonal polynomial contrasts were used to determine the most appropriate trend for the data. Statistical analysis was carried out in SPSS version 20 (IBM Corp. 2011).

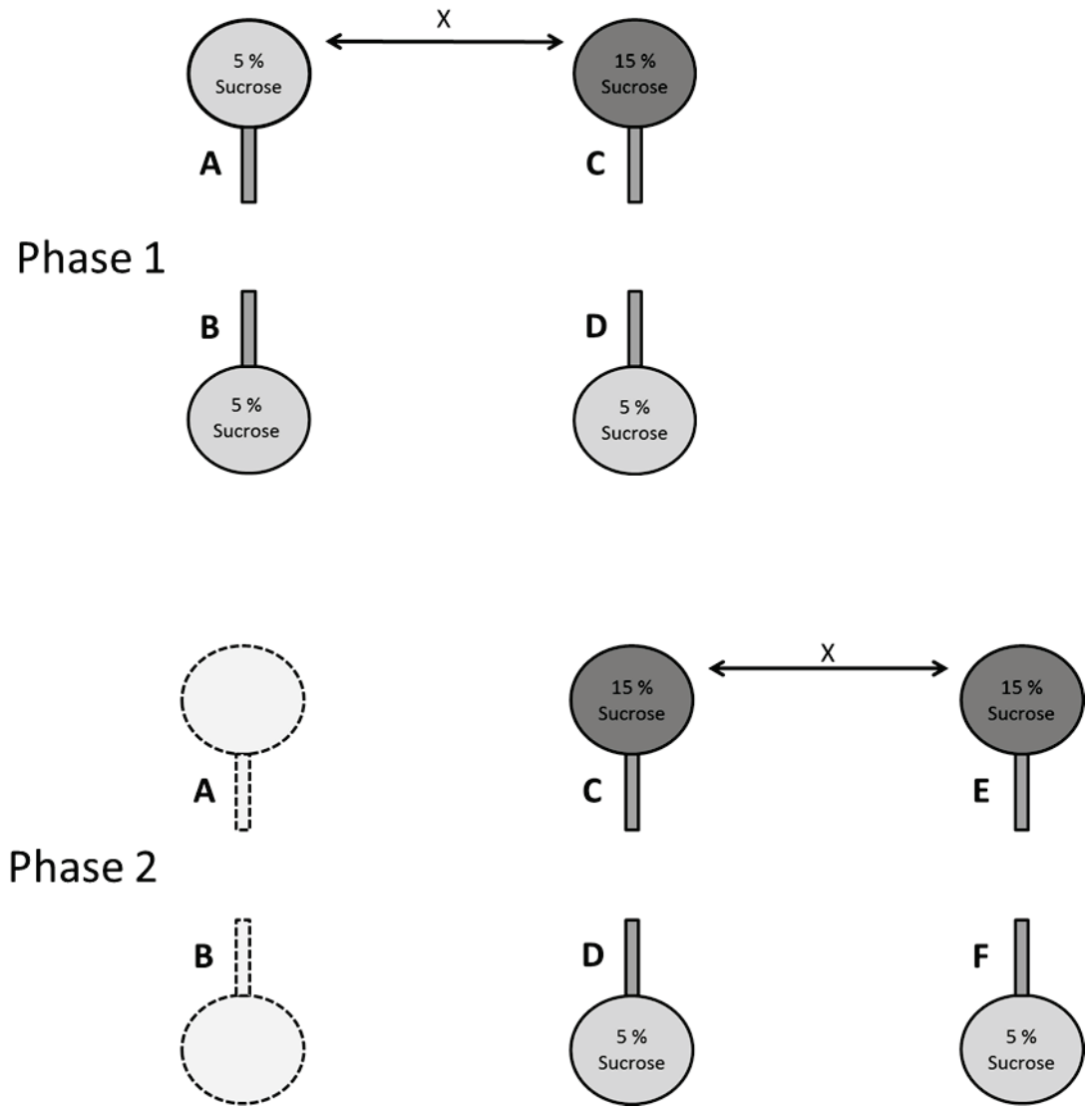

Figure 17: Array configuration used in experimental trials. In the initial array (Phase 1), feeder C contains the high concentration reward. Following displacement (Phase 2) feeder C still occupies the same absolute spatial location but feeder E occupies the same relative position within the array. Array spacing (X) was equal to the degree of sideways displacement in all cases. Perch orientation of each feeder is depicted.

6.4 Results

Initial visitation following displacement of the feeder array targeted the relative or absolute position of the high concentration reward in 93% (54/58) of cases across the four trials. The absolute location

of the originally rewarded feeder was selected more often than expected by chance (0.25) in the 100 cm ($p < 0.001$), 85 cm ($p < 0.001$) and 70 cm trial ($p = 0.034$), but not in the 55 cm trial ($p = 0.633$). The relative location of the original reward feeder was selected more often than expected by chance (0.25) in the 55 cm trial ($p = 0.027$) but not in any of the larger trials (1 m; $p = 0.836$, 85 cm; $p = 0.676$, 70 cm; $p = 0.287$).

The results of the Generalised Estimating Equation indicated that array size had a significant effect on strategy choice ($X^2_3 = 11.07$ $p = 0.011$). Polynomial contrasts suggested that a linear trend was most appropriate to describe this relationship (Linear contrast estimate = 0.41 ± 0.12, $X^2_1 = 11.55$, $p = 0.001$). As the size of the array increased, more participants responded to absolute spatial information and fewer attended to relative spatial information (Figure 18: Initial feeder choice following feeder displacement. Initial choice is presented as the percentage of individuals in each trial that adopted a relative or absolute strategy following feeder displacement.).

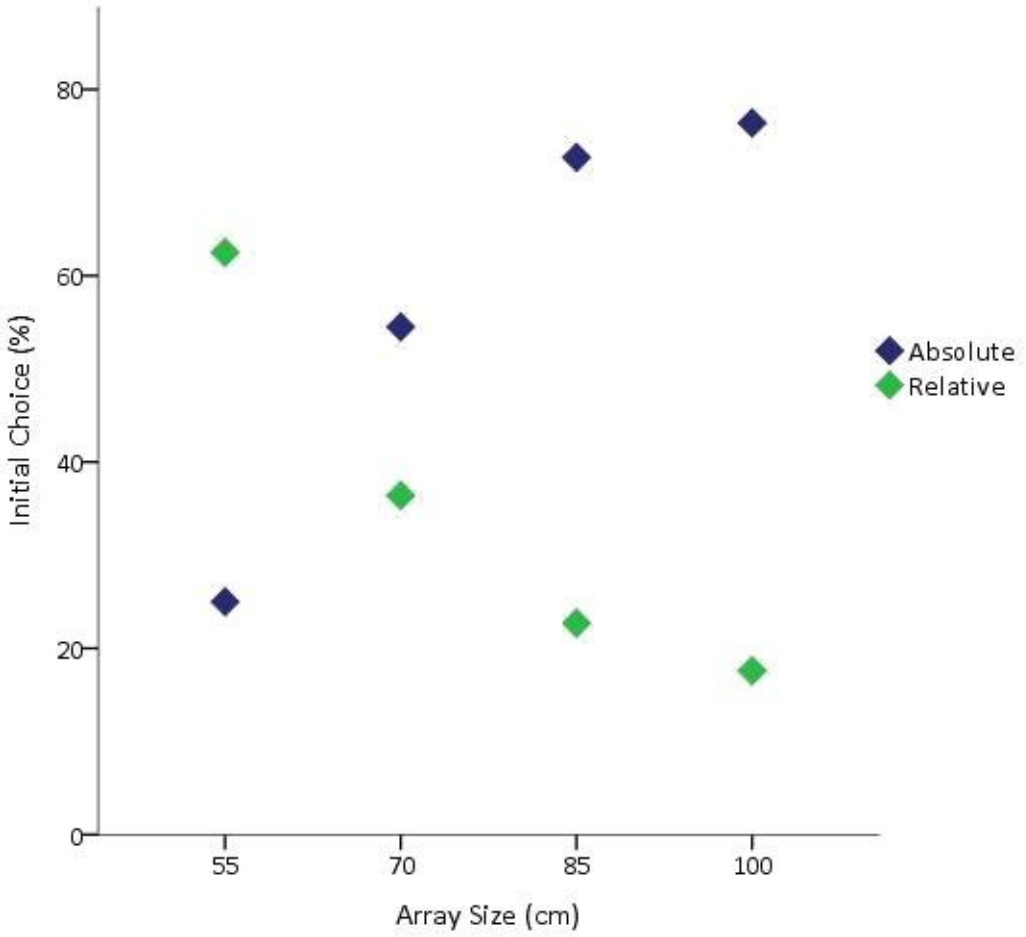

Figure 18: Initial feeder choice following feeder displacement. Initial choice is presented as the percentage of individuals in each trial that adopted a relative or absolute strategy following feeder displacement.

6.5 Discussion

Bellbirds appeared to use different spatial strategies to relocate rewards when foraging in arrays of different sizes. An absolute spatial strategy was favoured after displacement in the three largest experimental arrays (70 cm, 85 cm & 100 cm) suggesting greater reliance on global features of the environment. As the size of the array decreased, the importance of intra-array, local cues appeared to increase. In the smallest array (55 cm), a relative spatial strategy was favoured by participants. Multiple spatial representations are often acquired simultaneously so that there is a degree of redundancy in the spatial information that is encoded (Vlasak 2006; Legge et al. 2009). Dominant

strategy choice probably reflects the outcome of overshadowing between competing relative and absolute cues rather than an absence of alternative information (Legge et al. 2009). Relative position, although primarily dictated by the position of local landmarks (in this case, intra-array position), cannot be encoded without some directional input from extra-array or ego-centric cues, as each feeder has a symmetrical twin (A & D, B & C, Figure 17). Dominance of an absolute spatial strategy in the 70, 85 and 100 cm trials suggests that global cues were probably favoured by bellbirds participating in prior experimental trials [Chapter 4 and 5]. In Chapter 5, the location of a highly rewarding feeder was signalled by a visual cue which would have functioned as a local cue. Lower salience of local cues may have contributed to observed spatial priority, where visual cues were only utilised in novel arrays [Chapter 5].

The results of my study may indicate a distance threshold below which local, relative position cues overshadow global, absolute position cues. Two prior studies have also demonstrated a similar distance threshold for use of local, intra-array, and global, extra-array, cues (Healy & Hurly 1998; Thiele & Winter 2005). Hurly & Healy (1998) demonstrated that, following array displacement, rufous hummingbirds (*Selasphorus rufus*) foraging in large arrays (40 cm and greater) primarily returned to the absolute location of experimental flowers but that relative floral positions were favoured in smaller arrays. Thiele & Winter (2005) observed a similar effect in the Commissaris's long-tongued bat (*Glossophaga commissarisi*) where feeders with spacings of less than 20 cm were remembered as relative positions but at 40 cm and greater the absolute position was preferred. The presence of a distance threshold for spatial cue use may be indicative of a point at which global cues no longer provide sufficient spatial resolution to accurately re-locate a reward (Cheng & Spetch 1989). Alternatively, as all three species occupy a nectivorous niche, the distance threshold may be indicative of variation in floral foraging strategies across different spatial scales.

Nectivorous species experience variation in rewards at both between and within-plant level (Pacini & Nepi 2007). Switching to a reliance on intra-array cues in smaller arrays may indicate a point at

which flowers are perceived as part of a group element. Local cues may be more informative at a within-plant scale as variation in nectar reward is often determined by flower age, sexual stage, or position (Rathcke 1992), which can be detected by birds in close proximity to the flowers. Supporting the idea that local cues are of greater importance when foraging within plants, Pérez et al. (2011) found that hummingbirds foraging on natural flowers showed greater reliance on nearby, visual cues when foraging within a plant than between plants. Bellbirds use of visual, local cues, as examined in Chapter 5, may have been stronger had the experimental trials been conducted across smaller spatial scales (< 55 cm).

Findings from this pilot study are preliminary due to low trial replication. In particular, each array size was tested at a single, and unique, location, so I cannot rule out the possibility that availability of suitable natural landmarks differed between the locations without additional trials. However, the linear relationship between array size and preference for absolute location suggests this wasn't the case, and the results are in agreement with prior research on nectarivores (Healy & Hurly 1998; Thiele & Winter 2005; Pérez et al. 2011). Overall, the prevalence of an absolute spatial strategy suggests that the majority of informed foraging decisions made by bellbirds, e.g. tree choice and patch choice, are guided by spatial cues that are detectable for some distance from the location in question. Local cues, which were only favoured in one trial, appear less important overall, but may provide additional accuracy when making fine scale foraging decisions, e.g. within-plant foraging. Similar mechanisms may be used to remember other important non-feeding locations, such as nest sites. These findings have implications for future studies of bellbird cognition because they suggest that accuracy of spatial encoding may be influenced by environmental surroundings: some environments, e.g. aviaries, may not provide suitable global cues. Habitat structure may also affect the efficiency of memory informed foraging by bellbirds in natural environments.

Future research should seek to replicate these trials in unique environments to ensure that observed spatial strategies were not the result of site specific biases. Replication is especially relevant in the

case of fine scale relative location cue use, as this strategy was only favoured in one trial. It will also be important to quantify which natural features, both global and local, are utilised as spatial cues by foraging birds and how this information is encoded. Investigation of local, relative cues may be possible through manipulation of artificial cues that are close, but external, to closely spaced feeder arrays. Examination of global cues would require landmark manipulation on a larger scale and will only be possible in controlled or semi-controlled environments (Deipolyi et al. 2001; Vlasak 2006; Shang et al. 2015).

6.6 Conclusion

Bellbirds relied on cues provided by natural features that were external to the experimental array (global cues) to return to the absolute location of a highly rewarding feeder in the majority of experimental trials (70 cm, 85 cm, and 100 cm). Local cues regarding relative position, provided by features of the experimental array, were favoured in the smallest experimental array only (55 cm). These preliminary findings may indicate the presence of a distance threshold for absolute versus relative spatial cue use, as has been suggested for other nectivorous species.

Chapter 7

General Discussion

The availability and distribution of foraging resources can shape the evolution of dependant species and populations (Pravosudov & Clayton 2002; Sulikowski & Burke 2011). In some cases, selection forces can drive change at a neurological level, leading to cognitive specialisation of foraging behaviour (Healy & Krebs 1993; Pravosudov & Clayton 2002; González-Gómez et al. 2014; Rosati 2017). Exploitation of spatially scattered resources, including nectar, is often associated with an increased capacity for spatial memory (Henry & Stoner 2011). The ability to remember where and when nectar rich flowers will be available, based on past experience, typically allows for more efficient extraction of resources at a variety of scales (Henry & Stoner 2011; Pérez et al. 2011).

Prior research on cognitive specialisation by nectarivores has predominantly examined highly specialised, obligate species, with a particular focus on hummingbirds (Henderson et al. 2001; González-Gómez et al. 2011; González-Gómez et al. 2014). Most avian nectarivores exists in less specialised systems than hummingbirds (Zanata et al. 2017) and research on cognitive specialisation in Trochilidae may not be applicable to facultative nectivores in many cases. In this thesis I have explored information use and cognition in relation to New Zealand bellbirds. Bellbirds, despite bearing some morphological adaptations to nectar feeding, occupy a largely facultative nectar feeding niche that makes them good candidates for study of cognitive specialisation in a less specialised system.

7.1 Informed foraging movements

Informed foragers are able to increase their foraging efficiency by exploiting the environment in an optimised fashion (Stephens 2007; Bracis et al. 2015). Informed exploitation of resources typically creates distinct patterns of movement with respect to the spatial and temporal distribution of

resources (Garber 1989; Ohashi & Thomson 2009; Bracis et al. 2015). In Chapter 2 and 3, I examined bellbird movements with respect to the availability of nectar across two spatial scales. In Chapter 2, I demonstrated that bellbirds were capable of tracking the spatial distribution of resources at a local scale. Bellbirds modified their foraging behaviour to reflect the spatial distribution of nectar within a 1 ha area. This behavioural response appears flexible in its application, with high value, ornithophilous species eliciting a stronger tracking response. Seasonal trends in bellbird abundance, observed in Chapter 2, were in agreement with Spurr et al. (2011) who suggested that bellbirds leave Port Hills reserves over winter to exploit adventive nectar sources in Christchurch City. In Chapter 3, I quantified these large scale movements in male birds using a dialect matching technique. Dispersal from Port Hills source populations was found to be largely influenced by proximity. If resource tracking occurs is occurring at larger spatial scales (Spurr et al. 2011, 2014), it is most likely to be occurring at a patch scale within this expanded range, rather than across a landscape scale due to limited dispersal distances.

7.2 Mechanisms of information use

In Chapter 2, I demonstrated that bellbirds made informed foraging movements at a local scale. In Chapters 4 to 6 I examined the potential mechanistic basis of this information use by assessing bellbirds cognitive abilities through a series of experimental feeder trials. In Chapter 4, I demonstrated that bellbirds could use spatial memory to recall the location of a highly-rewarding feeder within an experimental array. Accurate short term recall of information was observed across all concentration treatments (7-20%), but retention intervals were found to be dependent on reward value. This flexible response to spatial information retention supports the findings of my local tracking trial (Chapter 2) as it demonstrates differential investment in information on the basis of perceived value.

In Chapters 5 and 6, I examined the role of information priority. When foraging under natural conditions, bellbirds would likely have access to information from multiple sources, simultaneously. In situations where two sources of information conflict, one source will usually be favoured at the expense of the other. Cue priority dynamics are important to consider because they provide insight into the strategies most likely employed under natural foraging scenarios. In Chapter 5, I demonstrated that, although bellbirds are capable of learning visual cues to locate a reward, spatial information was prioritised. Spatial priority indicates that, when relocating isolated nectar rewards (Spurr et al. 2010) or tracking resources (Chapter 2), bellbirds are likely to be largely reliant on spatial information (Chapter 4).

In Chapter 6, I examined information priority with regard to spatial scale. Bellbirds were shown to rely on more distal cues when foraging within large arrays, but favoured local cues when foraging in small arrays. Both spatial strategies were effective at relocating nectar rewards, but may be indicative of bellbirds employing an alternative strategy for locating nectar at a within plant scale. Visual cues, examined in Chapter 5, may be more important at a within plant scale, as they would function as local, or proximal cues.

A key theme that emerged in the course of these experimental feeder trials was the influence that New Zealand's unique flora may have played in shaping the cognitive abilities of bellbirds. Bellbirds, and other New Zealand nectarivores, consume nectar of highly variable quality (Bergquist 1987) from flowers which are often inconspicuous in appearance (Godley 1979; Castro & Robertson 1997). These factors may have contributed to bellbirds' ability and motivation to retain spatial information about low value resources (Chapter 4) and their slow acquisition of learnt visual associations (Chapter 5).

7.3 Summary of key findings

Bellbirds, despite behaving as generalists in many New Zealand environments, have cognitive abilities which have typically been associated with highly specialised nectarivores: they can track the spatial distribution of high value resources (Chapter 2), have accurate spatial memory recall (Chapter 4), and demonstrate spatial priority over visual information (Chapter 5). The main divergence from previous studies of highly specialist and obligate nectarivores, is that bellbirds are flexible with respect to the application of these cognitive skills as they showed greater investment in retention and recall of information for high value resources (Chapter 2 and 4). Flexible information use with regard to resource quality has not been demonstrated in other, more specialized, species and likely stems from the ability of bellbirds to switch to alternative food sources when nectar is unavailable, or unprofitable. These findings have relevance for the wider understanding of the nectivorous guild as they represent a more realistic system for many nectarivores than the highly specialised hummingbird system. Informed foraging in nectivorous birds that consume varied diets, such as sunbirds and other honeyeaters, may be more influenced by motivational constraints than, as has been previously emphasized, cognitive abilities.

7.4 Future directions

This study has taken a broad approach to examining information use by bellbirds and allowed key areas of interest to be identified across multiple spatial scales. This study was limited in detail in some areas, especially with regard to the role of social dynamics and constraints in information use. Future research should take a more focused approach to examine the intricacies of the information use concepts identified in this study.

7.4.1 Informed foraging movements

Research on informed foraging movements (Chapter 2 and 3) was conducted exclusively in Canterbury, where bellbirds are at a relatively lower density compared to other regions in New Zealand (Spurr et al. 2010), and do not face competitive exclusion by tūī. These factors may have influenced the role of competition and aggression in mediating bellbird movements. In other regions of New Zealand, informed movements may be restricted by greater behavioural interference. This may limit the expression of tracking movements or alter the spatial scale at which it is expressed. It would be beneficial to conduct similar trials in environments where bellbirds face greater interference and competitive stress. Mainland forests on the south and west coasts of the South Island may be good candidates for this type of study as both bellbirds and tūī are abundant in these regions. Managed island populations may also be alternatives as they have high population densities and limited nectar resources, e.g. Tiritiri Mātangi, but these populations face additional constraints on movement as a result of their isolation.

7.4.2 Mechanisms of information use

I have identified key mechanisms of information use by individual, adult male bellbirds. Future research should examine variation in information use with regard to social transmission and population demographics.

Work in this thesis has focused on the role of private information. Socially acquired information, which is gained indirectly by monitoring conspecifics' behaviour (Dall et al. 2005), may also play a role in influencing the bellbird relationships with nectar resources. Based on observations made throughout this study, I suggest that research into social networks, and information transfer between generations may be important starting points for examining the role of socially transmitted information.

Experimental trials were largely limited to adult male birds because females were infrequent visitors to supplementary feeder sites. Sexual dimorphism in cognitive ability has been noted in some species of hummingbird (González-Gómez et al. 2014), so would be beneficial to examine in greater detail with regard to bellbirds. Two female individuals participated in feeder trials in the course of this thesis, and although initial results appear to indicate that they also rely on spatial memory to locate nectar rewards, there was insufficient data to analyse with confidence (Appendix E). I believe that targeting feeder trials immediately prior to and during the breeding season, or using captive birds, would allow for sufficient replication to examine female birds. Differential use of information by juvenile birds (Franks & Thorogood 2018) could also be examined by conducting trials during the breeding season.

7.5 Applications of research

Understanding the cognitive capability of species is important from a management perspective as it has consequences for predicting likely behavioural responses and movement patterns (John et al. 2016; Kozlovsky et al. 2017). Concepts identified in this study could be developed to assist in the following management applications.

1. Bellbird reintroductions

Bellbird reintroductions often meet with mixed success. It is thought that this is predominantly due to the halo effect, where translocated individuals disperse too far from the release site to facilitate the formation of stable populations (Richardson et al. 2015). Provision of permanent supplementary feeders at release sites has been largely unsuccessful at mitigating dispersal, due to high levels of competitive exclusion by territorial male birds (Cresko 2010). It may be possible to achieve the desired constant food supply, without having it concentrated in a single, defensible location, by focusing on provision of high value natural resources in a manner which encourages local resource tracking.

2. Bait avoidance

Bait colour is generally regarded to be an effective cue for avoidance learning in birds (Werner et al. 2008). New Zealand based studies have focused on the efficacy of different colours as deterrents to feeding, but not as cues for avoidance learning (Cowan & Crowell 2017). The results of Chapter 5 indicate that bellbirds learnt positive visual associations more slowly than has been reported in other nectivorous species, which may also translate to slower learning of negative associations. If, as speculated in Chapter 5, slow learning of visual cues derives from the low prevalence of conspicuous floral signals in the New Zealand flora, this may be a widespread issue for bait avoidance in New Zealand.

3. Pollination limitation

Bellbirds are important pollinators of some New Zealand plant species, especially in Canterbury where tūī are rare. Several studies from Canterbury have suggested that ornithophilous species in Canterbury are becoming pollination limited due to low visitation by honeyeaters (Montgomery et al. 2001; Murphy & Kelly 2001; Robertson et al. 2008). Bellbirds appear motivated and capable of remembering the spatial location of high value resources, so it would appear that low pollination rates are an issue of nectar discovery and low, localised bellbird population numbers. Bellbirds did not appear to search at a landscape scale for nectar resources as dispersal was seemingly governed by proximity to breeding areas in most cases (Chapter 3). Increased discovery of nectar sources, and pollination, probably requires bolstering local populations through predator control or increased connectivity.

7.6 Strengths and weaknesses of study design

This study has taken a broad approach to examining information use by bellbirds, focusing on processes across a variety of spatial scales. In Chapter 2, information use is considered at a local scale, in Chapter 3 at a landscape scale, and in Chapter 4-6 at a fine experimental scale. This is both a

key strength of the overall body of work, and an important weakness to consider. Broadly examining information use at a variety of scales allowed identification of the most important concepts across a potentially vast research topic. This was important as there was minimal previous literature available to directly indicate the most appropriate scale of approach for honeyeaters. An inappropriate scale of focus may have resulted in important concepts, e.g. value of information, and processes, e.g. resource tracking, being overlooked.

The broad approach was also the main weakness of this study as it compromised detail at each level of investigation. As previously mentioned, lack of investigation into the role of social factors in information use may limit the applicability of these findings. My work indicates that bellbirds have the cognitive ability to use information to improve foraging success, but without an understanding of how this expression may be constrained by social factors, it is not known whether behaviours would be observed to the same extent outside of the Canterbury environment. Another limitation of this research is that I was unable to quantify how the concept of resource value translates to a natural system, which is a key step in applying the findings of my research further (Appendix A). Resource value can vary in many ways and I focused on concentration because it was the easiest to manipulate in an experimental setting. The value of natural nectar resources may be affected by other factors, including floral abundance, accessibility, nectar volume, rate of replenishment, or duration of flowering. When examining how bellbirds and other facultative nectarivores interact with their environment, these plant characteristics may be important factors to consider in understanding the role of resource value. The problem of quantifying natural resource value can be considered with reference to two important ornithophilous species, kowhai (*Sophora microphylla*) and fuchsia (*Fuchsia excorticata*). Both species are presumed to produce high quality nectar (Spurr et al. 2011) but have different strategies of floral production (Appendix A). Kowhai individuals flower intensively over a shorter time, whereas fuchsia produces flowers over a longer period. In this case variation in value is likely more complicated than variation in nectar characteristics, e.g. it may be

worthwhile to invest more effort into updating and retaining information about kowhai resources as the potential benefit, or cost of poor timing, may be higher.

7.7 Concluding remarks

Bellbirds are capable of using information gained from their environment to increase the efficiency of nectar extraction. Informed foraging was most sensitive to variation in nectar availability at a fine scale within experimental trials and at a local (1 ha) scale within native bush patches. Despite consuming nectar on a largely facultative basis in many environments, bellbirds performed comparably to more specialised species across a variety of cognitive trials. Adaptation to a facultative consumer niche appears not to have resulted in lower cognitive capabilities, rather in the flexible application of cognitive skills. Resource specific motivation is likely to play a large role in mediating responses to nectar in this species, and may be relevant for facultative nectarivores in other systems also. The broad approach of this study, although compromising detail in some areas, has allowed identification of several key themes across multiple spatial scales, and developed diverse methodologies for use in future studies.

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Appendix A

Plant characteristics as determinants of resource value

Research in this thesis suggests that the cognitive responses of foraging birds are dependent on perceived resource value (Chapter 2, Chapter 4). In natural environments, perceived resource value is likely to be influenced by factors beyond pollination syndrome (Chapter 2) and concentration (Chapter 4), including floral abundance, duration of flowering, sugar composition, sugar content, nectar variability and floral structure. A small pilot study was conducted at Kennedys Bush Reserve to examine variation in flowering characteristics in relation to three key ornithophilous species; kowhai (*Sophora microphylla*), fuchsia (*Fuchsia excorticata*) and flax (*Phormium tenax*). Three similar sized individuals of each species were monitored at intervals of 3 – 4 days during the period from September 2016 – January 2017. Floral characteristics were assessed with regard to three key traits.

Floral abundance: The total number of flowers present on each focal tree was estimated visually during each monitoring visit.

Sugar concentration: The sugar concentration of nectar from five individual flowers was recorded during each monitoring visit. Concentration was measured using a handheld, low volume Brix refractometer.

Sugar Content: A gravimetric technique was used to assess the total sugar content of floral nectar. Immature flowers on each focal tree were enclosed in fine mesh bags (10 flowers on each Kowhai and Fuchsia plant, 5 flowers on each Flax plant). Once flowers matured, nectar was extracted using dried, and weighed pieces of filter paper. The changes in mass of the filter paper segments after re-drying was used as an estimate of total carbohydrate content per flower.

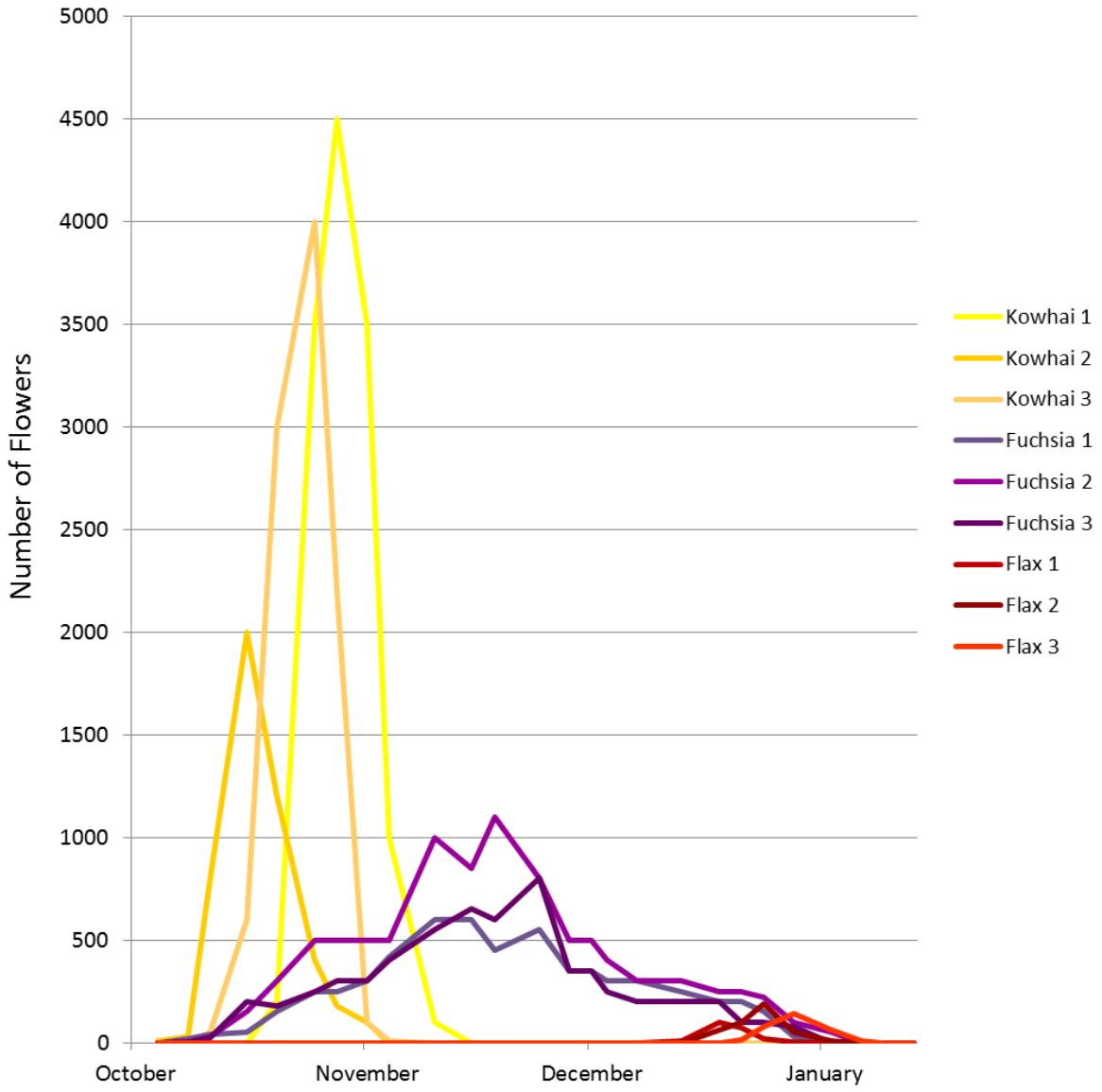

Figure A. 1: Floral abundance throughout the flowering period for monitored kowhai, fuchsia and flax individuals.

Table A. 1: Nectar characteristics of kowhai, fuchsia and flax.

Species	Concentration (%)	Sugar weight (mg)
Kowhai	21.91 ± 0.18	2.526 ± 0.240
Fuchsia	15.21 ± 0.12	1.701 ± 0.148
Flax	17.10 ± 0.28	4.412 ± 0.349

The results of this pilot study suggest that key ornithophilous species adopt different flowering strategies (Table A.1; Figure A.1). Kowhai and flax produced high quality nectar over short timeframes which is indicative of a 'big-bang' phenological strategy (Stewart & Dudash 2017). Fuchsia produced lower quality nectar rewards over an extended time frame which is more indicative of a 'steady-state' phenological strategy (Stewart & Dudash 2017). The 'big-bang' strategy may be associated with greater investment in information acquisition and retention by consumers because the potential payoff for optimally exploiting this resource is high but requires temporal precision.

Unfortunately, this study could not be progressed as the Port Hills fires of 2017 destroyed the vegetation on these plots.

Appendix B

Source population recording locations

Table A. 2: Location of acoustic recording sites in Port Hills reserves (Chapter 3). Automatic recording devices were deployed at each of these sites in order to detect source population dialect groups. The dominant song type detected at each location is indicated. Sites where no appropriate vocalisations were detected (no melody type), and sites where appropriate vocalisations were detected, but did not match with the three main shared types (no shared type) are also indicated.

Recorder Location	Latitude	Longitude	Dominant Song Type
Ahuriri Reserve	-43.666132	172.623766	Type C
Omahu Bush Reserve 1	-43.665488	172.611168	Type C
Omahu Bush Reserve 2	-43.661878	172.622184	Type C
Omahu Bush Reserve 3	-43.661624	172.622193	Type C
Omahu Bush Reserve 4	-43.66087	172.619412	Type C
Living Springs	-43.650788	172.624484	Type C
Cass Peak 2	-43.636272	172.618468	Type C
Cass Peak 1	-43.63668	172.622008	Type C
Kennedys Bush Reserve 1	-43.628181	172.623189	Type B
Kennedys Bush Reserve 2	-43.628794	172.623266	Type B
Kennedys Bush Reserve 3	-43.624706	172.61826	Type B
Kennedys Bush Reserve 4	-43.634799	172.625394	Type B
Ohinetahi Bush Reserve 1	-43.625266	172.629563	Type B
Ohinetahi Bush Reserve 2	-43.623616	172.634991	Type B
Ohinetahi Bush Reserve 3	-43.624034	172.635571	Type B
Hoon Hay Scenic Reserve	-43.621624	172.636228	Type B
Worlsey Spur	-43.622137	172.63071	Type B
Sugarloaf Scenic Reserve 1	-43.61227	172.64289	Type A
Sugarloaf Scenic Reserve 2	-43.606521	172.645948	Type A
Sugarloaf Scenic Reserve 3	-43.604527	172.651364	Type A
Victoria Park	-43.591613	172.64328	Type A
Bowenvale Recreation Reserve 1	-43.602145	172.658759	Type A
Bowenvale Recreation Reserve 2	-43.590923	172.662086	Type A
Bowenvale Recreation Reserve - Bush Head	-43.596876	172.657561	Type A
Bowenvale Recreation Reserve - Scott Reserve	-43.597448	172.66458	No melody type
Rapaki Valley	-43.597649	172.678267	Type A
Major Hornbrook Reserve	-43.588637	172.721905	Type A
Jollies Bush Scenic Reserve	-43.586541	172.739177	No shared type
Rapanui Bush Reserve	-43.593799	172.747809	No shared type

Appendix C

Urban acoustic recording locations

Table A. 3: Urban locations at which source population song types were detected (Chapter 3). Locations are a mixture of manual recording sites and sites where automatic recording devices were deployed. All song types detected are indicated. In locations where multiple types were detected, song types are listed in order of numeric dominance. Sites at which the shared unknown song type was detected (unknown type) are also indicated.

Recorder Location	Latitude	Longitude	Song Types Present
Cashmere A	-43.5801	172.6326	Type A, Type B
Cashmere B	-43.5633	172.634	Type A, Type B
Cashmere C	-43.5755	172.6271	Type A
Somerfield	-43.5655	172.6116	Type A
Cracroft	-43.5706	172.6185	Type A
Westmorland	-43.5807	172.6046	Type A
Hillsborough	-43.5676	172.6546	Type A
St Martins	-43.5618	172.6634	Type A, Type B
Ferrymead	-43.5608	172.7088	Type A
Heathcote	-43.5712	172.689	Type A
Bowenvale	-43.5664	172.6278	Type A
Botanic Garden	-43.5303	172.62	Type A
Horseshoe Lake	-43.5034	172.6737	Type A
Halswell A	-43.5984	172.5785	Type B
Hoon Hay	-43.5726	172.5936	Type B
Halswell B	-43.5845	172.5737	Type B
Broadfield	-43.6168	172.5226	Type B
Ladbrooks	-43.599	172.5121	Type B
Tai Tapu A	-43.6063	172.5666	Type B
Tai Tapu B	-43.6445	172.5564	Type C
Lincoln	-43.642	172.4519	Type C
Lincoln	-43.6432	172.469	Type C
Riccarton Bush	-43.5374	172.5945	Unknown Type
Sumner	-43.5719	172.7744	Unknown Type
Styx Mill	-43.467	172.61	Unknown Type
Styx Mill	-43.463	172.6014	Unknown Type
Travis Wetland	-43.4894	172.6879	Unknown Type
North New Brighton	-43.4927	172.7034	Unknown Type
Bottle Lake Forest	-43.4679	172.6815	Unknown Type
The Groynes	-43.4476	172.6103	Unknown Type

Appendix D

Christchurch unknown type

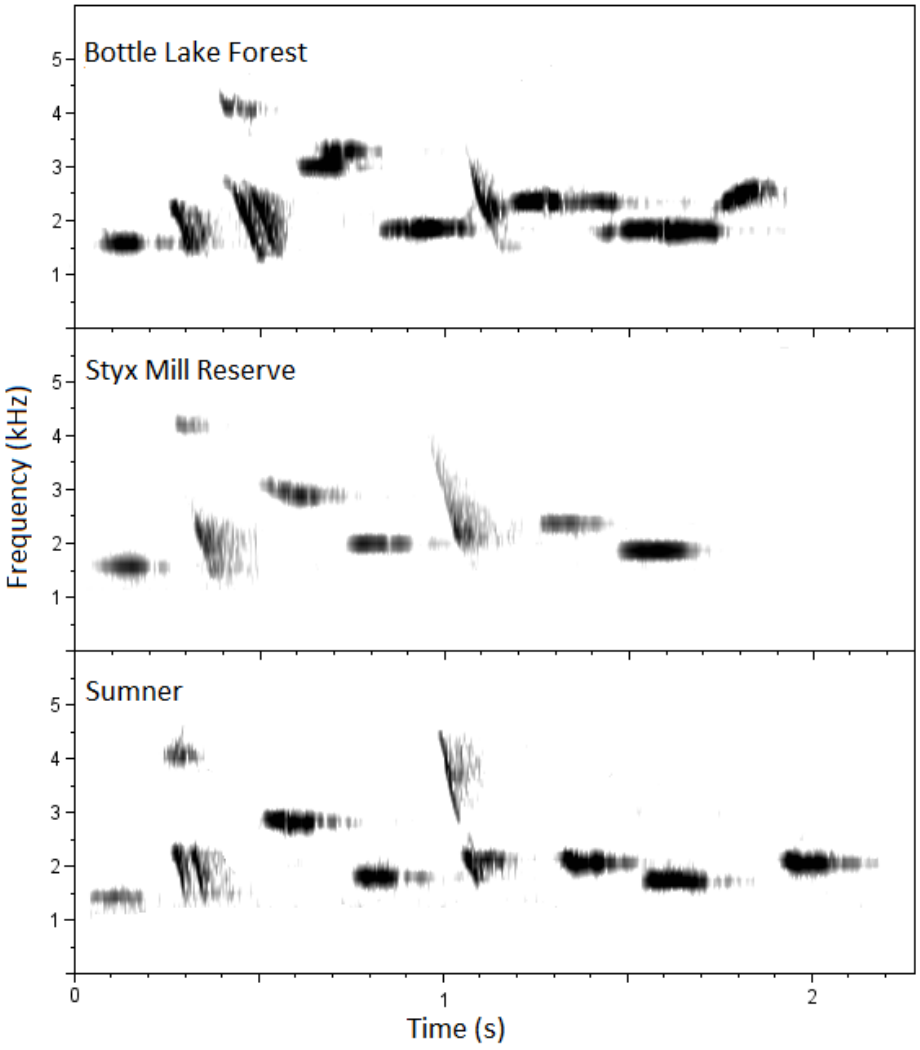

Figure A. 2: Spectrograms depicting the unknown shared song type, which was recorded across eight locations in northern and eastern Christchurch (Chapter 3). Example songs are from north-eastern Christchurch (Bottle Lake Forest and Styx Mill Reserve) and south-eastern Christchurch (Sumner).

Appendix E

Spatial memory in female bellbirds

Females were rare visitors to experimental arrays (Chapter 4 – 6). Two adult females made repeated visits to experimental arrays during the short-term spatial memory trials conducted as part of Chapter 4. In these trials, the ability of individuals to remember the location of a high concentration feeder (HCF) amongst an array of three less rewarding feeders (5%) was assessed across four HCF concentration treatments; 7%, 10%, 15% and 20% sucrose. Preliminary results from the pair of female birds suggest that females were able to use spatial memory to relocate rewards. Bout accuracy, the percentage of return phase visitation bouts in which the first visit to the array was to the HCF, ranged from 88.2% to 96.2%. The figure below depicts the female bout accuracy in relation the spread of accuracy data from all male birds. Female data was within the limits of male data for all concentration treatments (Figure A. 4).

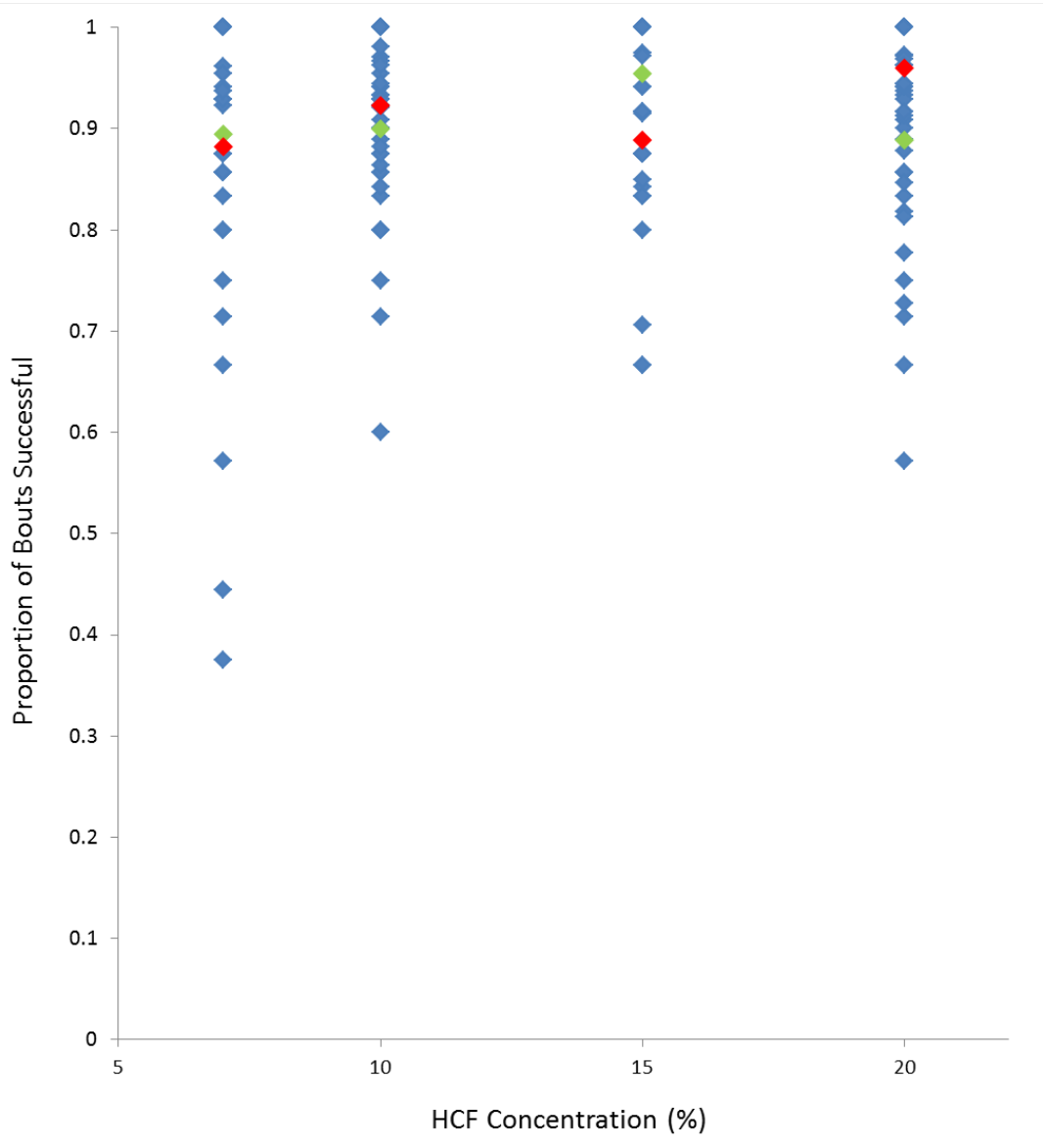

Figure A. 3: Bout accuracy of male and female birds in spatial memory trials. Data from male birds is depicted by blue markers, data from the two female birds is depicted by the red (Hermione) and green (Molly) markers.

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